A synthesis of animal-mediated seed dispersal of palms reveals distinct biogeographical differences in species interactions

Muñoz, Gabriel; Trøjelsgaard, Kristian; Kissling, W. Daniel

Published in:
Journal of Biogeography

DOI (link to publication from Publisher):
10.1111/jbi.13493

Publication date:
2019

Document Version
Publisher's PDF, also known as Version of record

Received: 26 March 2018 | Revised: 24 October 2018 | Accepted: 13 November 2018

DOI: 10.1111/jbi.13493

RESEARCH PAPER

WILEY Journal of Biogeography

A synthesis of animal-mediated seed dispersal of palms reveals distinct biogeographical differences in species interactions

Gabriel Muñoz[1] | Kristian Trøjelsgaard[2] | W. Daniel Kissling[1]

[1]Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, Amsterdam, The Netherlands

[2]Faculty of Engineering and Science, Department of Chemistry and Bioscience, Section of Biology and Environmental Science, Aalborg University, Denmark

Correspondence
W. Daniel Kissling, Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, The Netherlands.
Email: wdkissling@gmail.com

Present address
Gabriel Muñoz, NASUA, Andrade Marin E7-76 & Diego de Almagro, 170135, Quito, Ecuador.

Funding information
SENESCYT; University of Amsterdam; University of Amsterdam Faculty Research Cluster 'Global Ecology'; Netherlands Organisation for Scientific Research, Grant/Award Number: 824.15.007

Editor: Lisa Manne

Abstract

Aim: To synthesize published knowledge on palm–frugivore seed dispersal observations and to test whether broad-scale differences in geographic coverage, diversity, composition and functional structure of plant–animal interactions emerge between biogeographical regions.

Location: Neotropics and Afrotropics.

Methods: We constructed a meta-network for both regions by aggregating observations of pairwise palm–frugivore interactions from the primary literature. We assessed sampling completeness with accumulation curves and estimated knowledge gaps for individual palm species and geographic units within biogeographical regions. We compared the taxonomic composition as well as structural indices of regional interaction networks and tested whether functional trait matching (i.e., the relationship between palm fruit size and frugivore body size) differs between regions.

Results: A total of 750 unique pairwise interaction records were retrieved from the primary literature covering 340 frugivores and 126 palms. Sampling completeness of frugivore interactions within biogeographical regions and for individual palm species was low (often <50%), geographic coverage limited, and relative knowledge gaps were largest in areas with high palm species richness. Interaction diversity and network modularity was larger in the Neotropics than the Afrotropics. A positive fruit size–body mass relationship (i.e., functional trait matching) was statistically significant in the Afrotropics, but not in the Neotropics.

Main conclusions: Available data on palm–frugivore interactions suggest major biogeographical differences in ecological networks among regions, even when taking differences in palm species richness into account. The Neotropics showed a larger interaction diversity and more modular network structure than the Afrotropics. Broad-scale morphological trait matching among plants and frugivores was only observed in the Afrotropics. The lack of a Neotropical trait matching relationship might be driven by the late Quaternary extinctions of mammalian megafauna in this region. Although our work has increased the digital availability of palm–frugivore

interaction observations, massive knowledge gaps of interaction diversity remain in the tropics.

KEYWORDS
animal-mediated seed dispersal, Arecaceae, biotic interactions, data sharing, ecological networks, Eltonian shortfall, frugivory, functional trait matching, multispecies interactions, mutualism

1 | INTRODUCTION

Quantifying knowledge gaps in digitally accessible information is a priority for advancing biodiversity science (Hortal et al., 2015; Meyer, Kreft, Guralnick, & Jetz, 2015). One of the key gaps is the lack of knowledge about interactions among species or groups of species (Hortal et al., 2015). Although interest in studying species interactions over broad spatial extents is increasing (Araújo & Rozenfeld, 2014; Schleuning et al., 2014; Trøjelsgaard & Olesen, 2013; Zanata et al., 2017), comprehensive datasets on ecological networks are still restricted to a few study sites, limiting many applications in biogeography and macroecology (Kissling & Schleuning, 2015; Poisot et al., 2016). Nevertheless, a considerable—yet underutilized—portion of our current knowledge on species interactions can be found within the published scientific literature (de Almeida & Mikich, 2018; Poelen, Simons, & Mungall, 2014). This information can be extracted from the text, but is usually not readily accessible in a digital format (Skusa, Rüegg, & Köhler, 2005; Thessen & Parr, 2014). Once extracted, such interaction data might provide an avenue for a deeper integration of macroecology and network research, for example by analysing the structure and functional composition of aggregated meta-networks (de Almeida & Mikich, 2018; Hagen et al., 2012; Kissling & Schleuning, 2015).

One of the key mutualistic interactions among plants and animals is frugivory, that is when animals, especially vertebrates, consume fleshy fruits and subsequently disperse the seeds (Fleming, Breitwisch, & Whitesides, 1987; Fleming & Kress, 2013; Kissling, Böhning-Gaese, & Jetz, 2009). Animal-mediated seed dispersal is particularly ubiquitous in the tropics where up to 90% of the plant species in a particular community might rely on fruit-eating vertebrates for seed dispersal (Fleming et al., 1987). Recent research on fleshy-fruited plants and frugivores has revealed that interactions among these mutualistic partners are often constrained by functional traits (Bender et al., 2018; Dehling, Jordano, Schaefer, Böhning-Gaese, & Schleuning, 2016). For example, fruit size limits the fruit ingestion by relatively small-sized seed dispersers, and the size of the ingested fruits therefore tends to be positively correlated with body sizes and gape widths of consumers (Jordano, 2000; Lord, 2004; Onstein et al., 2017). Nevertheless, there is considerable variation in functional traits among biogeographical regions (Fleming & Kress, 2013; Mack, 1993) and it remains an open question whether functional trait matching in plant–frugivore interactions can be consistently observed across regions (Bender et al., 2018; Onstein et al., 2017).

With >2,500 species, the palms (Arecaceae) are a major plant family and characteristic of tropical and subtropical regions across the world (Dransfield et al., 2008). Due to decades of research, palms have received a comprehensive taxonomic scrutiny (Govaerts & Dransfield, 2005) and many aspects of their ecology, biogeography and evolution have been widely studied (Baker & Couvreur, 2013; Eiserhardt, Svenning, Kissling, & Balslev, 2011; Henderson, 2002; Kissling et al., 2012). Moreover, palms are a keystone resource for frugivorous animals in the tropics because they provide a large amount and wide variety of fruits to animal consumers (Fleming & Kress, 2013; Henderson, 2002; Onstein et al., 2017; Zona & Henderson, 1989). Seed dispersers of palms include many frugivorous animals, including birds, bats, non-flying mammals, reptiles, insects, and even fishes (Zona & Henderson, 1989). Zona and Henderson (1989) provided the most comprehensive review of animal seed dispersers of palms, and despite updates of this work (http://www.virtualherbarium.org/palms/psdispersal.html), we still know little about how palm–frugivore interactions differ among biogeographical regions and where knowledge gaps are most pronounced. Key questions are to what extent the strong differences in palm species richness between the Afrotropics (e.g., mainland Africa with 65 species, and Madagascar with 175 species) and the Neotropics (>700 species) (Kissling et al., 2012) as well as the regional differences in the taxonomic and functional trait composition of avian and mammalian frugivores (Kissling et al., 2009, 2014) are reflected in macroecological patterns of palm–frugivore interactions (Kissling, 2017). Moreover, identifying knowledge gaps could help to prioritize targeted efforts for new and more intensive data collection.

Here, we synthesize published knowledge on frugivore seed dispersal of palms in the Afrotropics and the Neotropics and quantify biogeographical differences in palm–frugivore interactions between both regions. We focus on those two biogeographical regions because they differ strongly in both species richness and traits of palms and frugivores (e.g., Kissling, 2017; Kissling et al., 2009, 2012; Onstein et al., 2017; Sandom et al., 2013) and because biogeographers have a great interest in explaining the diversity anomalies among these regions (Fleming & Kress, 2013; Fleming et al., 1987; Mack, 1993; Richards, 1973). Using interactions recorded in the primary literature, we aggregate information on species interactions to quantify the geographic, taxonomic, and functional variation in palm–frugivore interactions. Specifically, we explore (a) to what extent this information is incomplete and unevenly distributed in geographic space (Hortal et al., 2015; Meyer et al., 2015), (b) whether taxonomic and biogeographical differences in palms and frugivores drive

differences in the structure and composition of the aggregated meta-networks (Kissling et al., 2009, 2012, 2014), and (c) whether functional trait relationships between palms and frugivores are consistent across both biogeographical regions. Furthermore, we also aim to enhance the digital availability of species interaction data (Poelen et al., 2014) by increasing accessibility, interoperability, and reusability (Wilkinson et al., 2016).

2 | METHODS

2.1 | Data compilation

We first extracted interaction data from the literature (Figure 1, green boxes). Candidate articles were selected from a comprehensive literature search in Thomson's Web of Science (WoS) in January 2016. We used the following combinations of English search terms: "seed disper" and/or "africa" and/or "palm" and/or "southameric" and/or "neotropic" and/or "afrotropic." Since the WoS has not all titles and full-text available in English, we repeated the same search by replacing the terms "seed disper" and "southameric" with the corresponding translations in Portuguese, Spanish, and French (i.e., languages widely used in the study regions). For instance, we included the search terms "dispersao," "sementes," "dispersion," "semillas," and "graines" as translations of "seed dispersal."

From this literature search, we compiled an initial list of 2,232 articles (Figure 1). Each reference was labelled with a random alphanumerical code using the ZOTERO software (www.zotero.org). Since full text scans (by manual reading) are very time consuming, we screened the abstracts and titles of all articles from this initial list and pre-selected those articles for further consideration that mentioned potential information on palm–frugivore interactions and/or seed dispersal in the title or abstract. We did this pre-selection screening using the abstract_screener() function from the R package 'metagear' (Lajeunesse, 2015). This R package provides a graphical user interface that allows visualizing abstracts and titles and creating a database with references without seeing the names of journals and authors (thereby avoiding potential publication selection biases based on author name, journal, or year of study). The pre-selection screening resulted in 692 references for a manual full text scan (Figure 1). This resulted in extracting pairwise seed dispersal interactions between palms and frugivores from 162 articles (Figure 1).

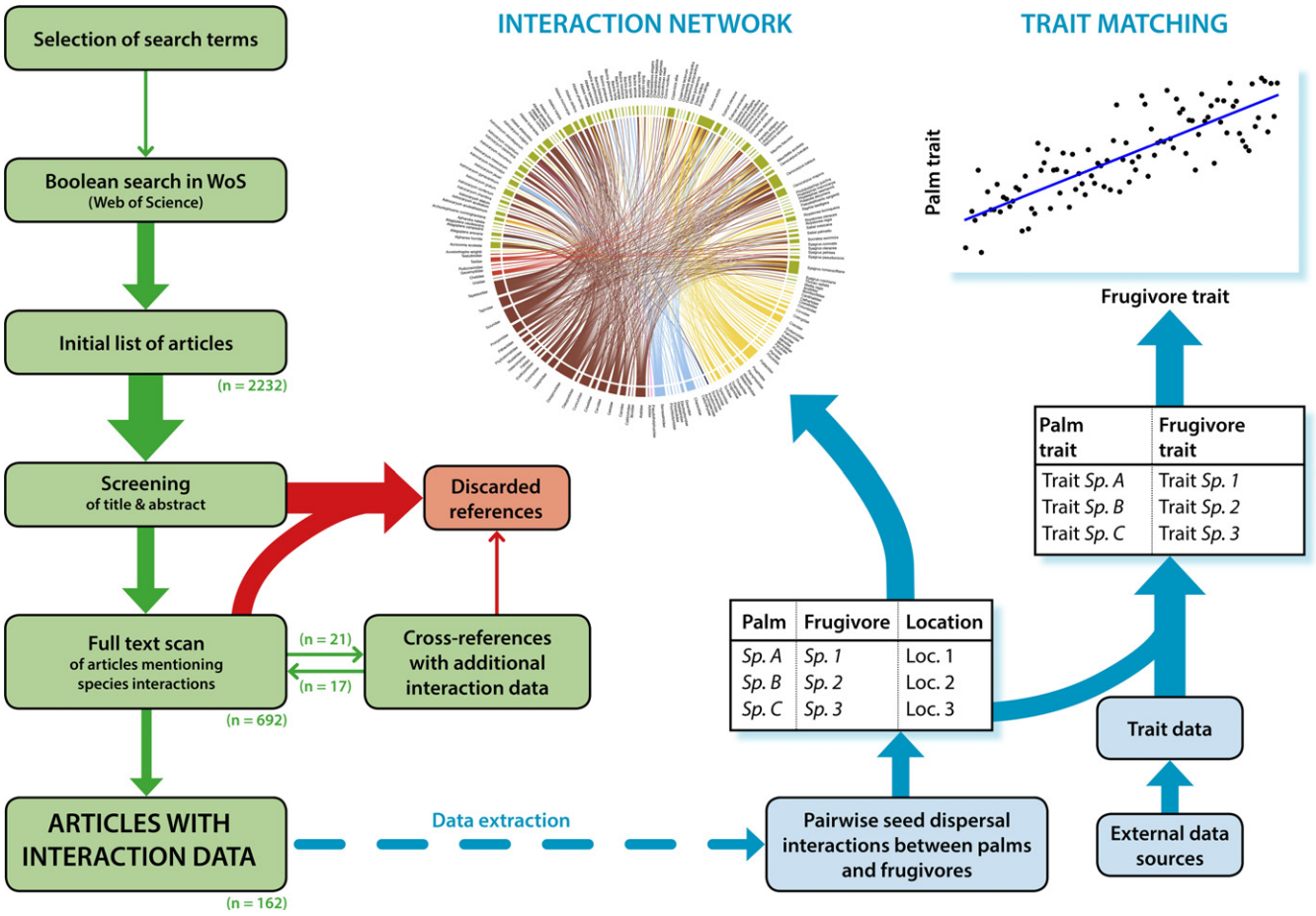


FIGURE 1 Workflow to extract and analyse pairwise palm–frugivore interactions from the literature. Left (green boxes): extraction of interaction data from articles through literature search, title and abstract screening (with R package 'Metagear'), full text scans and cross-references to other articles. Increasing arrow sizes reflect larger number of articles. Right (blue boxes): aggregation of pairwise interaction data into meta-networks and analyses of trait matching using additional data on frugivore body size and palm fruit size [Colour figure can be viewed at wileyonlinelibrary.com]

Appendix S1 in Supporting Information lists the data sources (except those that are already cited in the main text).

For the data extraction, we recorded an interaction when an article mentioned the fruit or the seed of a palm being dispersed, carried or defaecated by a frugivorous animal. Hence, we did not only focus on endozoochorous seed dispersal but also on seed dispersers that do not swallow the seeds, for example bats and scatter-hoarding rodents that usually carry large fruits. We further aimed to only record effective seed dispersal interactions, that is avoiding interactions that reflect seed predation. In most cases, a clear difference between seed disperser and seed predator was made in the examined articles because seed predators typically destroy the seeds during consumption. However, for some taxa (e.g., parrots) the relative importance of seed predation versus seed dispersal remains debated (Tella et al., 2015). We also included secondary dispersers such as scatter-hoarding rodents which take the fruits from the ground. Interactions were only recorded if the specific palm species occurred in the Neotropics or Afrotropics, not in other biogeographic regions. Most observations of pairwise species interactions could be extracted from the article text or from tables. Interactions were not included if species-level information was unavailable for either the palm or the frugivore (e.g., general statements such as "hornbills and primates consume fruits of palm A" were not included).

The dataset obtained from our literature search included the palm–frugivore seed dispersal data from Zona and Henderson (1989). We additionally included the latest update of this dataset (from July 2006) which is only available online (http://www.virtualherbarium.org/palms/psdispersal.html). From all examined articles, we further extracted basic meta-data information, including the year of publication, journal name, and location where the interaction was observed.

To standardize the taxonomic names of palms, we followed the World Checklist of palms (Govaerts & Dransfield, 2005), using an updated version (downloaded July 2015). For birds, we followed the BirdLife Taxonomic Checklist v8 (BirdLife International, 2015). For mammals, we followed the taxonomy from the IUCN Red List (IUCN et al., 2008). All other species names of animal seed dispersers were standardized according to the Integrated Taxonomic Information System (ITIS, https://www.itis.gov/). Besides species names, we also extracted information on the taxonomic class and order for each palm and frugivore using the tax_name() function from the R package 'taxize' 0.7.4. (Chamberlain & Szöcs, 2013).

In the second part of the workflow (Figure 1, blue boxes), we aggregated all pairwise interaction data extracted from the 162 articles and combined it with location and trait data of palms and frugivores. To extract information on functional traits (see below), we used external data sources (i.e., not from the articles from which interaction data were extracted). We focused on measures of fruit size for palms and body size for frugivores (a proxy of gape width) because size matching is the most commonly reported morphological trait matching relationship in plant–frugivore interactions (Bender et al., 2018; Burns & Lake, 2009; Dehling et al., 2016; Donatti et al., 2011; Eklöf et al., 2013; Jordano, 2000; Lord, 2004; Mack, 1993; Onstein et al., 2017).

2.2 | Quantification of knowledge gaps

We quantified knowledge gaps in digitally accessible palm–frugivore interactions by (a) estimating sampling completeness, and (b) assessing geographic coverage of interaction data.

Sampling completeness was estimated for each biogeographical region (Neotropics, Afrotropics) as the ratio between the total observed frugivore richness and the expected asymptotic value as derived from a species richness estimator (i.e., the expected richness of frugivorous dispersers for all palm species) (Rivera-Hutinel, Bustamante, Marín, & Medel, 2012). Given the heterogeneous nature of our sampling, we selected the nonparametric incidence-based Chao estimator because it is among the best estimators for low sample sizes and it accounts for frequencies of rare species (Chao, Colwell, Lin, & Gotelli, 2009). The Chao estimator was calculated with the specpool() function from the R package 'vegan' 2.3.5 (Oksanen et al., 2007) which assumes a lognormal distribution of the variance to estimate the 95% confidence intervals around the expected asymptotic value. We further calculated accumulation curves with 100 random permutations of the sampling units (i.e., palm species) using the function specaccum() (with "method = random") from the R package 'vegan' 2.3.5 (Oksanen et al., 2007). We used palm species as the sampling units because they were the focal taxa for which interactions were extracted from the literature. Our implementations generally followed the approach suggested by Gotelli and Colwell (2001) and Rivera-Hutinel et al. (2012).

We also estimated sampling completeness of frugivore interaction information for each individual palm species. To do this, we quantified accumulation curves for each individual palm species by randomizing the unique records of frugivores using articles with interaction information as sampling units. Individual palm sampling completeness was estimated as the ratio between the observed palm degree and the expected degree (i.e., the asymptotic value of frugivores calculated with Chao). Sampling completeness was only quantified for palm species which interacted with at least two different frugivore species and for which interaction information was available from at least two articles. Frugivore records from reviews such as the one from Zona and Henderson (1989) were excluded because it was not possible to relate every single interaction record to the original article source. Subsequently, we investigated (with Spearman rank correlations and single predictor regressions) whether the number of articles in which a palm has been recorded was a good predictor of (a) palm degree (i.e., the total number of frugivores the palm interacted with), and (b) sampling completeness of individual palms. This was done to quantify potential publication bias, that is to test whether the amount of knowledge on interaction partners is related to the number of published articles.

To assess the geographic coverage of interaction data, we used location data from the articles (i.e., where the interaction was observed) and standardized them by assigning the location information to geographic units as defined by the Taxonomic Databases Working Group (TDWG) (Brummitt, 2001). We used the TDWG level 3 units ("botanical countries,") which mostly represent

countries, but some of the very large countries such as Brazil are subdivided into states or provinces. This is the finest spatial resolution at which global palm distribution data are currently available (Kissling et al., 2012). We calculated four metrics to assess geographic coverage because each of them gives different insights into the coverage of interaction data. First, we calculated the ratio of palm species with interaction data relative to the total number of palm species recorded in each botanical country (based on the World Checklist of palms, see above). This indicated how many palm species within a botanical country have at least some information on interaction partners (i.e., a minimum of one recorded interaction). Second, we calculated for each botanical country the total number of unique interactions (i.e., the number of pairwise seed dispersal interactions between a particular palm species and a particular frugivore species). This indicated how many unique interactions have been recorded in total for a particular botanical country. Third, we calculated for each botanical country the mean number of interactions recorded per palm species using all palm species present in a botanical country (i.e., including also palms without interaction data). Fourth, we calculated the mean sampling completeness of individual palm species for each botanical country. Here, we also used all palm species present in a botanical country (based on the World Checklist of palms) and assigned a sampling completeness of zero to palm species for which sampling completeness could not be estimated. This metric provides an estimate of how well, on average, palms are sampled (in terms of frugivore interactions) within a botanical country.

2.3 | Comparison of networks

The pairwise interaction data extracted from the literature were aggregated into two meta-networks: one for the Neotropics and one for the Afrotropics. Both meta-networks were binary two-mode matrices with *P* palm species in rows and *F* frugivores in columns. Each element (P_i,F_j) with species *i* and *j* in the binary adjacency matrices had a value of 1 if frugivore F_i had been observed to interact with palm species P_j, and zero otherwise. To compare the diversity and organization of species interactions within the two regional meta-networks, we calculated a number of commonly used network-level indices. The most simple indices included the number of palm and frugivore species, their ratio, the size of the interaction matrices (*P*×*F*), the total number of species (*P*+*F*), the total number of interactions (*I*), connectance (i.e., the ratio between realized and potential interactions given as $C=I/(P\times F)$), and the mean number of interactions per species (Table 1). These indices describe the size and diversity of the networks in terms of species and interactions (Trøjelsgaard & Olesen, 2013). We further calculated nestedness and modularity, two of the most commonly used network-level indices that describe the organization of species interactions within the entire network (Bascompte, Jordano, Melian, & Olesen, 2003; Fortuna et al., 2010; Olesen, Bascompte, Dupont, & Jordano, 2007).

Nestedness measures to what extent interactions of specialist species are proper subsets of the interactions of generalist species (Almeida-Neto, Guimarães, Guimarães, Loyola, & Ulrich, 2008; Bascompte et al., 2003). We calculated nestedness with the *NODF* metric proposed by Almeida-Neto et al. (2008) which is included in the bipartite package (Dormann, Fründ, Blüthgen, & Gruber, 2009) for R. The *NODF* metric ranges from 0 (not nested) to 1 (perfectly nested). To compare nestedness between networks, we standardized the empirical *NODF* values as *Z*-scores:

$$NODF_{Z-score} = \frac{(NODF - NODF_{null})}{SD_{null}}$$

where $NODF_{null}$ is the average *NODF*-value of 999 random matrices using a null model that re-ordered interactions while maintaining species richness and palm degree (i.e., the number of interactions). Hence, in this null model the probability of allocating an individual palm–frugivore interaction is ultimately dependent on the total number of interactions a specific frugivore has, with generalist frugivores having a higher probability of being selected than specialists. This null model corresponds to the 'r1' null model from the R package 'vegan' (Oksanen et al., 2007). The SD_{null} value represents the standard deviation. The $NODF_{Z\text{-}score}$ therefore measures the difference between empirical and random nestedness in numbers of standard deviations. Values at least 1.96 standard deviations away from the mean are considered to be statistically significant.

Modularity quantifies the degree to which a network is structured into independent or semi-independent subgroups (modules) of species within the network (Donatti et al., 2011; Olesen et al., 2007). We evaluated differences in modularity between networks by measuring modularity *Q* for each meta-network as defined by Barber (2007):

$$Q = \frac{1}{m}\sum_{i=1}^{P}\sum_{j=1}^{F}(A_{ij} - H_{ij})\delta(g_i, h_j)$$

where *m* is the total number of interactions when considering an adjacency matrix *A* of *P*×*F* dimensions where interactions are only allowed between F_i and P_j. H_{ij} is a null model matrix that describes the probability of occurrence of an interaction between *i* and *j* based on the degree distributions of A_{ij}. The δ refers to the Kronecker's delta function and equals 1 when individual species P_i and F_j are sorted into the same module. Species *i* and *j* are assigned to a community group or module, denoted by g_i and h_j. Modularity *Q* then measures the extent to which interactions are formed within modules instead of between modules (Barber, 2007; Olesen et al., 2007). *Q* ranges from 0 to 1, where higher values represent a stronger division of a network into modules of closely interacting species (Donatti et al., 2011; Olesen et al., 2007).

We used a Label Propagation Algorithm (LPAwb+) to calculate *Q* (Beckett, 2016). LPAwb+ works well for calculating modularity in binary bipartite networks and it can be integrated with the R software (Beckett, 2016). Since the LPAwb+ algorithm is sensitive to node label initialization, we analysed each network 100 times and selected the configuration with the highest *Q*. We further noted the number of modules and module affiliation for each species in this configuration. To test the significance of *Q*, we implemented a null model by calculating the distribution of *Q* values from 999 random matrices following the same procedure as for nestedness, that is, maintaining the matrix dimensions and assigning interactions

TABLE 1 Network-level indices that describe the diversity and organization of Neotropical and Afrotropical palm–frugivore networks. For the Neotropics, indices for both the full meta-network as well the mean (±SD) from subsampled networks (n = 100) are provided. The Neotropical network was subsampled to have the same number of palm species as the Afrotropical network

Index	Symbol	Neotropics meta-network[a]	Neotropics subsampled[b]	Afrotropics meta-network[a]
Number of palm species	P	98	29	29
Number of frugivore species	F	283	130 ± 30.98	57
Palm–frugivore ratio	P/F	0.34	0.23 ± 0.05	0.51
Network size	$P \times F$	27,930	2,709 ± 1,183	1,653
Total number of species	$S = P + F$	383	159 ± 25.6	86
Total number of interactions	I	660	188.5 ± 43.2	90
Connectance	$C \quad I/(P \times F)$	0.02	0.05 ± 0.004	0.05
Mean number of interactions per palm species	L_p	6.73	6.88	3.1
Mean number of interactions per frugivore	L_f	2.33	1.53 ± 0.12	1.58
Modularity	Q	0.5	0.60 ± 0.04	0.69
Standardized modularity[c]	$Q_{Z\text{-}score}$	18.48	9.07 ± 1.4	8.07 ± 0.56
Number of modules	N_M	69	27.11 ± 1.30	22
Nestedness	$NODF$	8.52	11.11 ± 2.69	7.47
Standardized nestedness[c]	$NODF_{Z\text{-}score}$	4.46	−2.70 ± 3.20	−2.46 ± 0.07

[a]Indices of the full meta-network as assembled from all collected pairwise palm–frugivore interactions in a biogeographical region.
[b]Average indices for the subsampled Neotropical networks which contained the same number of palm species (n = 29) as the full Afrotropical meta-network. The subsampling was repeated 100 times and the mean (±SD) of network indices is provided (see Methods for details).
[c]Standardized modularity and standardized nestedness were calculated as Z-scores against a null model calculating modularity (Q) and nestedness ($NODF$) from a set of 999 random matrices (see Methods for details).

proportional to the frugivore marginal totals (Almeida-Neto et al., 2008; Schleuning et al., 2014). Q values were standardized using Z-scores ($Q_{Z\text{-}score}$) and we considered those at least 1.96 standard deviations from the null model mean as significantly modular (Almeida-Neto et al., 2008).

To allow a direct comparison of network indices between biogeographical regions—independent of differences in network size—we subsampled the Neotropical network 100 times to the same number of palm species as the Afrotropical network. This was done because some network indices depend on network size (Rivera-Hutinel et al., 2012). We calculated the mean (±SD) of all indices across the 100 subsampled Neotropical networks and compared them to the indices of the full Afrotropical meta-network. For the Neotropics, we report the indices for both the subsampled networks and the full meta-network.

2.4 | Functional trait matching

To test for functional trait matching, we explored the relationships between palm fruit size and frugivore body size using generalized linear models. As a measure of fruit size, we extracted fruit length of palms (in cm) using available information from books (e.g., Henderson, 2002) and other sources, including monographs and species descriptions (e.g., references and data sources listed in appendix of Göldel, Kissling, & Svenning, 2015) as well as the palmweb database from the Royal Botanical Gardens, Kew (http://palmweb.org). For each mammalian and avian frugivore, we extracted average body mass (in g) for birds from Dunning (2008) and for mammals from Sandom et al. (2013). Since we did not have morphological measurements of gape width (which usually have to be obtained from museum specimens or individuals captured in the field), we used body mass as a proxy for gape width to describe the size matching relationship between frugivores and palms (Donatti et al., 2011; Mack, 1993; Onstein et al., 2017). Hence, we used palm fruit length (log-transformed) as the predictor variable and the median value of body masses of all frugivores eating, dispersing, carrying, or defaecating a particular palm species as response variable (log-transformed). We performed analyses for all frugivore species (mammals, reptiles, and birds) as well as separate analyses for the most commonly recorded disperser group (bird and mammal, respectively). There were no palms being mainly dispersed by reptiles. We further did these analyses separately for the Neotropics and the Afrotropics. Because palm species can be dispersed by frugivores from different animal classes, we assigned a particular palm species as being dispersed by either birds or mammals depending on the most commonly recorded taxonomic class of frugivore dispersers.

3 | RESULTS

3.1 | Data compilation

Our literature search resulted in an initial list of 2,232 articles. After screening of titles and abstracts, a total of 692 articles were selected for a full, manual text scan. From these articles, pairwise seed dispersal interaction data for palms and frugivores were found in 162 articles.

The assembled species interaction dataset comprised a total of 1,122 interactions, with 750 being unique pairwise interaction records. A total of 340 frugivore species and 126 palm species were involved. The vast majority of interactions was recorded from the Neotropics (1,008 in total, containing 660 unique interactions), involving a total of 98 palm species and 283 frugivore species. The Afrotropics had considerably less interaction data (114 in total, of which 90 were unique), and only involved 29 palm species and 57 frugivore species.

3.2 | Quantification of knowledge gaps

Accumulation curves of interactions for both biogeographical regions did not approach asymptotes (Figure 2a). This suggested that knowledge on palm–frugivore interactions in both regions is highly incomplete. Sampling completeness (i.e., the percentage of the total number of frugivores that are estimated to disperse all palm species in a region) was 47% for the Neotropics and 40% for the Afrotropics (Figure 2a).

At the level of individual palm species, estimated sampling completeness ranged from 14–100%, with an average of 57 ± 21% (±SD) across all palm species for which asymptotic values of the frugivore accumulation curves could be estimated (n = 49 species; Table S1). Hence, accumulation curves for individual palm species rarely approached asymptotes (Appendix S2 Figure S1), even not for palm species such as *Euterpe edulis* and *Syagrus romanzoffiana* that had the largest number of interaction partners recorded (i.e., 56 and 38 frugivores, respectively, see Table S1). The number of interactions per palm species showed a positive relationship with the number of articles in which interaction information was recorded for each palm species (Spearman rank correlation: Neotropics r = 0.84; Afrotropics r = 0.54) (Appendix S2 Figure S2). This could suggest a publication bias, that is, the number of recorded interactions of a palm depends on the amount of published articles. However, there was no relationship between individual palm sampling completeness and the number of articles having interaction records for a particular palm species (Figure 2b). These results suggest that although palms which are present in many articles also tend to have many interaction partners, they are not necessarily better sampled than palms present in a few articles. This could arise because widespread palms are more likely to interact with a larger pool of frugivores throughout their geographic range. Positive Spearman rank correlations between palm degree (number of frugivores) and the number of botanical countries a palm is present (Neotropics: r = 0.64; Afrotropics: r = 0.69) support this assumption.

Within regions, 57% of the botanical countries in the Neotropics and 23% in the Afrotropics (including Madagascar) had available information on palm–frugivore interactions (Figure 3). In most cases, the ratio of palm species with interaction records relative to the total number of palm species recorded in a botanical country was low, ranging from 0.02 to 0.25 (Figure 3a). However, in the Afrotropics some botanical countries with few (<5) palm species (e.g., Botswana, Zimbabwe and the Cape Provinces) had relative high ratios (Figure 3a). In the Neotropics, high ratios were observed in Brazil Southeast and Argentina Northeast (Figure 3a), botanical countries with 65 and 10 palm species, respectively. The total number of recorded interactions (Figure 3b) was highest in hyperdiverse botanical countries such as Brazil Southeast (containing the Atlantic Forest), Brazil North (containing the heart of the Amazon basin), and Colombia (with 224 palm species being the most diverse botanical country in the Neotropics). In the Afrotropics, the total number of unique palm–frugivore interaction records per botanical country was generally low (<20) (Figure 3b). The mean number of recorded interactions per palm species was highest in the Cape Provinces, Botswana and in the south-eastern part of the Neotropics (Figure 3c). When considering the mean sampling completeness of palm species within botanical countries, the Afrotropics (except Madagascar and the Cape Provinces) showed a higher average sampling completeness for individual palm species than the Neotropics (Figure 3d), reflecting the low diversity of both frugivores and palms in this region.

3.3 | Comparison of networks

The taxonomic composition of the two regional meta-networks differed strongly (Figure 4). The Neotropical meta-network was composed of palm species from 15 different palm tribes, with Cocoseae being the most represented tribe (55 species). It showed a broad range of taxonomic diversity among frugivores and included mammals, birds, reptiles, beetles, crabs, and fishes (Figure 4). Neotropical frugivores included tapirs, rodents, toucans, tanagers, cracids, macaws, parrots, and new-world monkeys, among others. The collared peccary (*Pecari tajacu*) and the white-lipped peccary (*Tayassu pecari*) interacted with the largest number of palm species (24 and 19 palm species, respectively).

The Afrotropical meta-network contained fewer palms and frugivores than the Neotropical one, and was taxonomically also less diverse because only birds and mammals appeared as seed dispersers of palms (Figure 4). Seven Afrotropical palm tribes were included in the network, and Areceae was the most species-rich tribe (10 palm species). The palm species *Elaeis guinensis* and *Phoenix reclinata* had the highest number of interactions as they were recorded to interact with 15 and 14 frugivores, respectively. Afrotropical seed dispersers of palms included parrots, hornbills, elephants, baboons, guenons, mangabeys and chimpanzees, with no single frugivore species standing out as dispersing a particular high number of palm species. In Madagascar, lemurs were the most important palm seed dispersers, especially for species in the palm genus *Dypsis*.

Most network-level indices showed considerable differences in the diversity and organization of species interactions between the two regions, even when the Neotropical network was subsampled to an equal number of palm species (Table 1). Specifically, the Neotropical meta-network included more frugivore species, more pairwise interactions, and a larger interaction matrix than the Afrotropics, and this remained true when subsampling the Neotropical networks (Table 1). After subsampling, connectance (i.e., the proportion of all

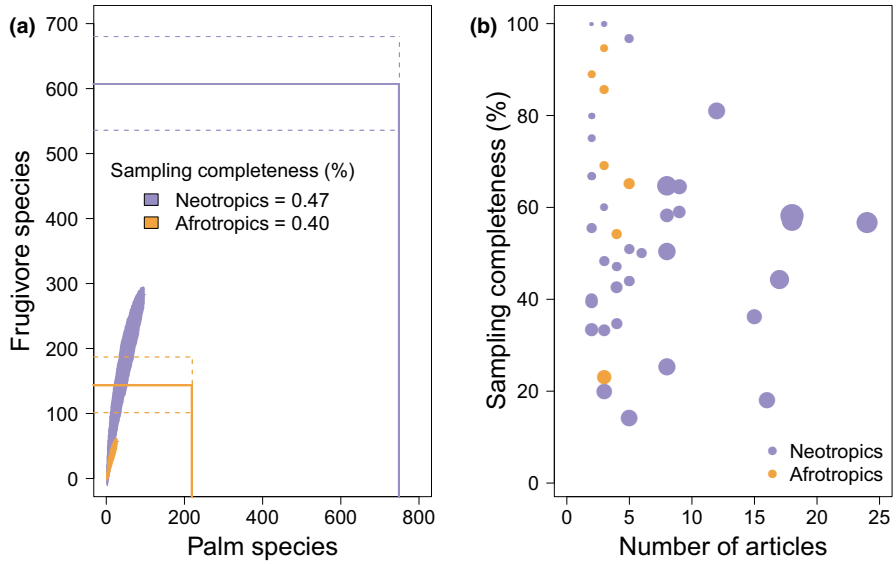


FIGURE 2 Sampling completeness of palm–frugivore interaction data in the Neotropics and Afrotropics. (a) Rarefied species accumulation curves obtained from randomizing palm species and estimating the asymptote value with the Chao species richness estimator. The stippled lines represent the variance around the expected asymptote. The vertical lines represent estimates of the total number of palm species actually recorded in each biogeographical region (*x*-axis) versus the estimated asymptote and its associated variance for the total number of frugivore species dispersing palm species in each region (*y*-axis). (b) Relationships between estimated sampling completeness of palm–frugivore interactions and the number of articles in which individual palm species have been recorded. Only palm species for which interaction information is available from at least two articles and two unique interactions are included (n = 49 species). Sampling completeness was quantified as the ratio between the expected number of frugivores and the observed number of frugivores for each palm species (see Appendix S2 Figure S1 for accumulation curves of individual palm species). The symbol size represents the decadic logarithm of the number of frugivores reported for each palm species [Colour figure can be viewed at wileyonlinelibrary.com]

potential interactions that are realized) was similar in the Neotropics and the Afrotropics (Table 1). Both regions also showed significantly modular networks (*Z*-scores > 1.96; Table 1). After subsampling, the mean standardized modularity ($Q_{Z\text{-}score}$) remained slightly larger for the Neotropics than the Afrotropics, although it had a large variance (Table 1). The Neotropical meta-network had a large number of modules (n = 69), the subsampled Neotropical networks on average consisted of 27 ± 1.30 (±SD) modules, and the Afrotropical network consisted of 22 modules (Table 1). The Neotropical meta-network was significantly nested (mean $NODF_{Z\text{-}score}$ in Table 1), but both the subsampled Neotropical networks and the Afrotropical meta-network were significantly anti-nested (with $NODF_{Z\text{-}score}$ <−1.96, Table 1).

3.4 | Functional trait matching

Overall, frugivores with larger body sizes tended to disperse palm species with larger fruits (Figure 5), but the relationship was only statistically significant in the Afrotropics (Table S2). In both regions, mammalian frugivores tended to disperse medium to large palm fruits whereas birds tended to disperse small to medium-sized fruits. However, considering birds and mammals separately, positive functional trait matching relationships between palm fruit size and frugivore body size were only statistically significant in the Afrotropics (Figure 5, Table S2). This suggests that biogeographical differences in traits of interacting species can determine the broad-scale structure of ecological networks.

4 | DISCUSSION

By aggregating pairwise interaction data from the scientific literature, we compiled a comprehensive palm–frugivore seed dispersal dataset for the Neotropics and the Afrotropics. Even when accounting for differences in palm species richness, the available data revealed considerable differences in palm–frugivore interactions between the two biogeographical regions, with the Neotropics having a broader taxonomic range, larger interaction diversity and stronger modularity than the Afrotropics. Functional trait analyses between palm fruit size and frugivore body size revealed that large-scale trait-matching relationships are only observed in the Afrotropics, indicating that larger palm fruits are dispersed by larger frugivores (both birds and mammals). Nevertheless, major knowledge gaps in interaction diversity remain in tropical regions where palms and vertebrate frugivores are particular diverse (Kissling et al., 2009, 2012, 2014).

Our analyses suggest that the amount of knowledge of observed palm–frugivore interactions is not merely driven by publication bias. Sampling completeness of individual palm species did not correlate with the total number of articles in which they were present. Hence, the most well-studied palms (which also have many interaction partners) tend to be the most abundant and widespread ones, and the wide geographic distribution allows them to interact with a larger diversity of frugivores. In both regions, the majority of the seed dispersers are mammals and birds, but the Neotropical meta-network also included reptiles, a land crab, one beetle, and ten fish species.

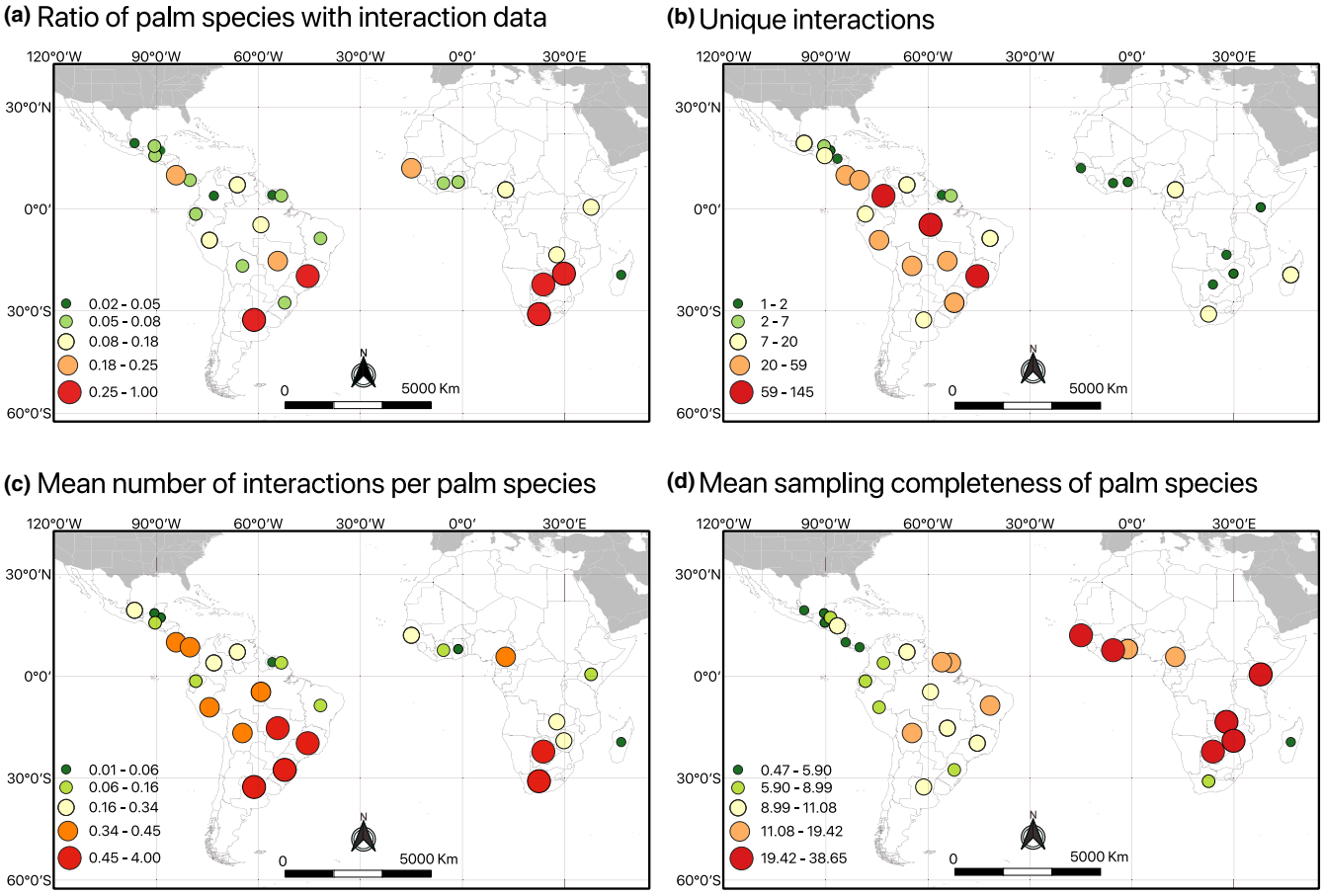
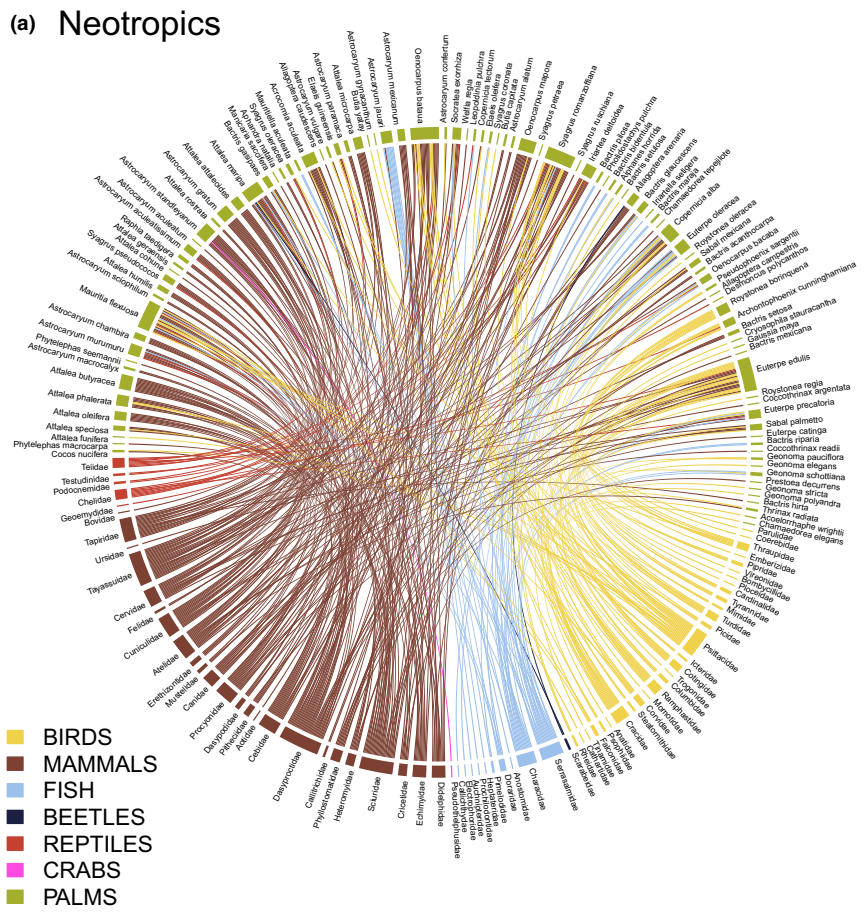


FIGURE 3 Geographic variation of palm–frugivore interaction information for the Neotropics and Afrotropics. (a) Ratio of palm species with interaction data (i.e., the number of palm species with interaction data relative to the total number of palm species present in each botanical country), (b) the total number of unique interactions (i.e., counting all pairwise interactions between a palm species and a seed-dispersing frugivore species), (c) mean number of interactions recorded per palm species within a botanical country (palms with no interaction records were included by assigning a value of zero), and (d) mean sampling completeness of individual palm species (palms for which sampling completeness could not be estimated were included and assigned a value of zero). Geographic units represent "botanical countries" as defined by the Taxonomic Databases Working Group (TDWG). Data are plotted for the geographic centroids of each botanical country (TDWG level 3 units) [Colour figure can be viewed at wileyonlinelibrary.com]

Fishes are important seed dispersers of Neotropical plants, including palms (*Astrocaryum*, *Bactris*, *Mauritiella*, and *Iriartella*) (Horn et al., 2011). In the Afrotropics, fishes have been recorded as fruit-eaters in the Congo basin for other plants (Beaune et al., 2013), suggesting that palm–fish interactions could in principle occur in this region. The most widely recorded mammalian seed dispersers of palms in the Neotropics were tapirs, peccaries, primates, scatter-hoarding rodents, and bats, whereas in the Afrotropics mostly primates and bats were recorded (including lemurs in Madagascar). The birds were mostly non-passerine species (~80%), with toucans, cracids, and parrots being commonly recorded in the Neotropics and hornbills and turacos in the Afrotropics. At the meta-network level, an important group of generalist species in the Neotropics were rodents, which were present in approximately one-third of the modules in this region. In the Afrotropics, primates were generalist species and represented in about half of all modules. In both regions, passerine birds tended to be specialists, interacting only with one or few palm species. Parrots were the most generalist bird group, being represented in about one-fifth of the modules. While it is generally assumed that parrots are seed predators and thus do not participate in seed dispersal mutualisms (Fleming & Kress, 2013), there is increasing evidence that many parrots do indeed disperse the seeds of plants, including palms (Tella et al., 2015). This indicates that parrots can serve as efficient long-distance seed dispersers, although their net effect on the population dynamics of their food plants will rely on the negative impact of seed predation versus the benefits derived from long-distance seed dispersal (Tella et al., 2015).

Network indices can be affected by network size (Rivera-Hutinel et al., 2012). For instance, connectance correlates negatively with network size and our subsampling showed that Neotropical networks had a similar connectance to the Afrotropical meta-network when subsampled to the same number of palm species. However, for modularity the standardized $Q_{Z\text{-}score}$ showed a statistically significant modular structure for all networks, that is the Neotropical meta-network, the subsampled Neotropical networks, and the Afrotropical meta-network. This suggests that seed dispersal

Journal of Biogeography



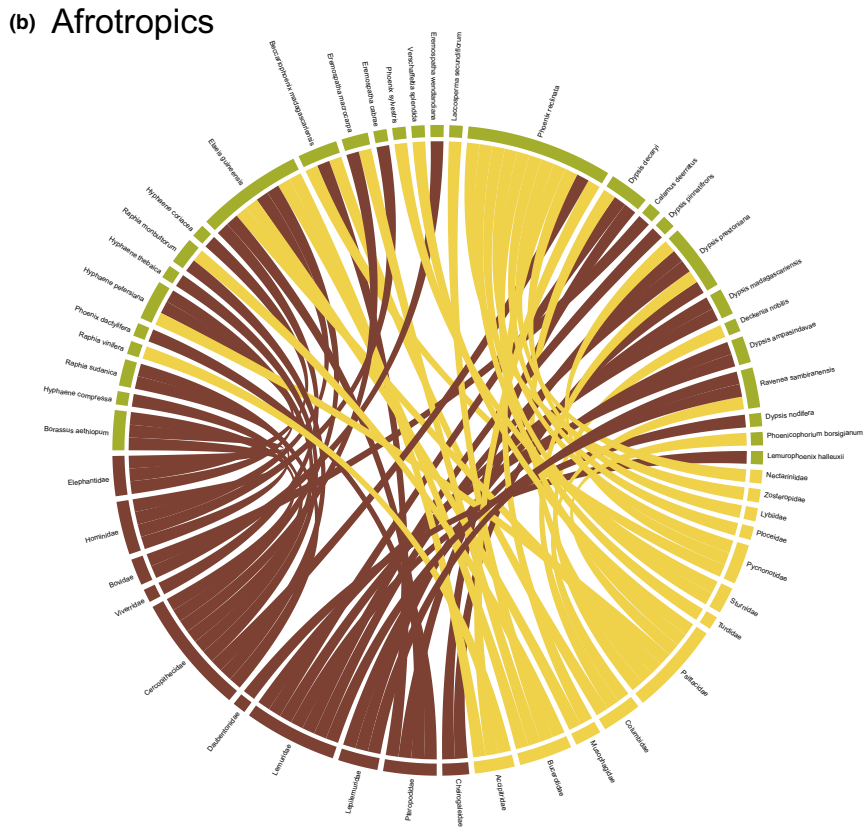


FIGURE 4 Regional meta-networks derived from aggregating pairwise species interactions between palms and frugivores as compiled from published literature. (a) Meta-network for the Neotropics (with 98 palms and 283 frugivores), and (b) meta-network for the Afrotropics (with 29 palms and 57 frugivores). Each line represents a recorded seed dispersal interaction between a palm species (green boxes, upper half) and frugivorous animals (other colours, lower half). Frugivores are grouped into taxonomic classes (mammals: brown; birds: yellow; reptiles: red; beetles: black; crabs: pink and fishes: light blue). The size of boxes for each palm and frugivore species is scaled in proportion to the total number of seed dispersal interactions recorded for each taxonomic group. Palm species are sorted clockwise with decreasing fruit size (i.e., large-fruited palms on the left, small-fruited palms on the right). Mammal and bird species were sorted clockwise with increasing body mass (large-bodied species to the left, small-bodied species to the right) [Colour figure can be viewed at wileyonlinelibrary.com]

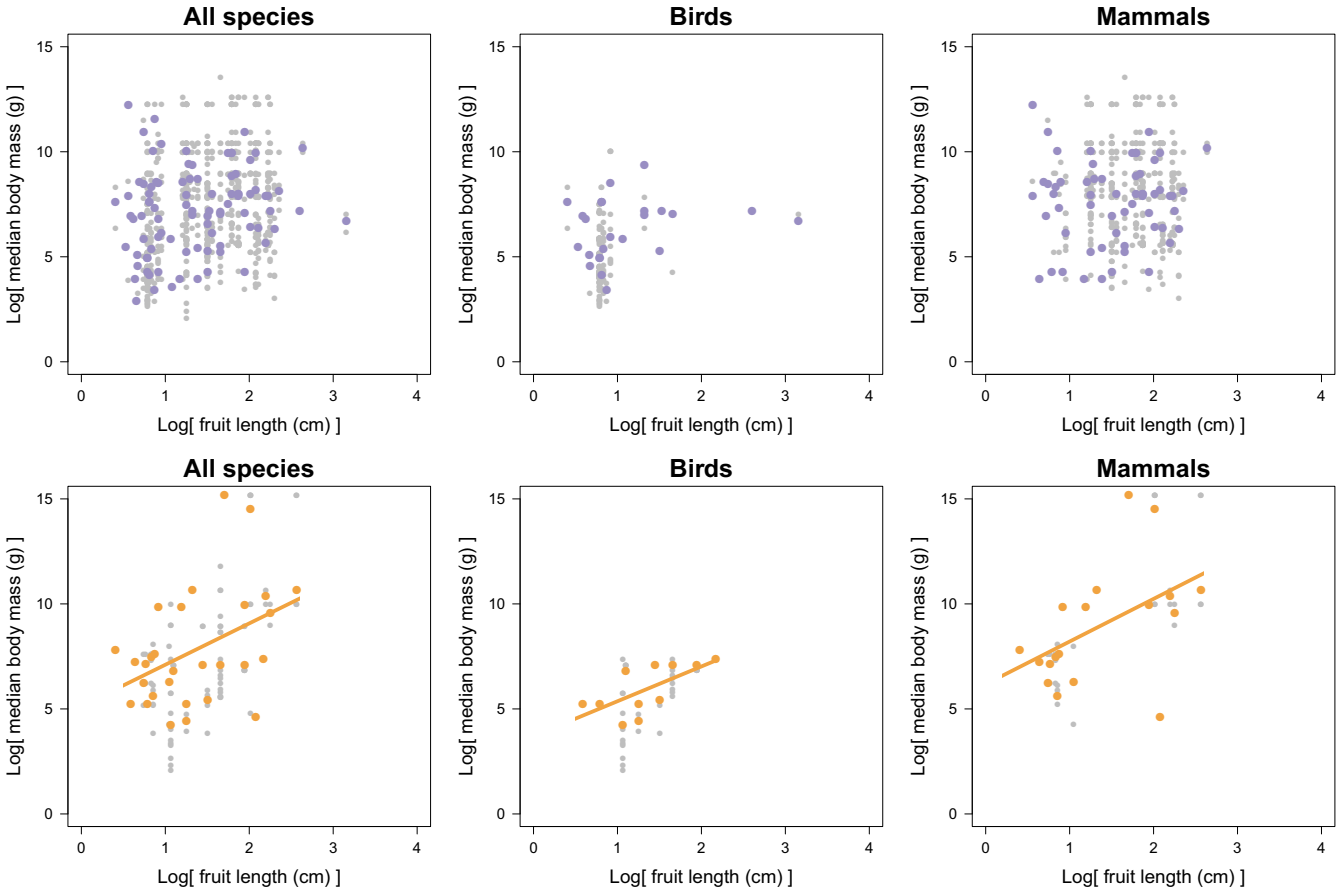


FIGURE 5 Relationships between frugivore body size (*y*-axis) and palm fruit size (*x*-axis) for the Neotropics (upper row) and the Afrotropics (lower row). The relationships are shown for all palm species dispersed by mammals, reptiles, and birds (left), palm species only dispersed by birds (middle), and palm species only dispersed by mammals (right). Fruit size of each palm species is represented by log-transformed fruit length (cm). Frugivore body size is represented by log-transformed median body mass (g) of all frugivore species that have been recorded to disperse a particular palm species. The median body mass values are given in colours (purple and orange) whereas grey points represent species-level variation of frugivore body mass. Lines represent statistically significant relationships between median frugivore body size and palm fruit size (see Table S2 for results from linear regressions) [Colour figure can be viewed at wileyonlinelibrary.com]

interactions between palms and frugivores at macroscales are formed by cohesive groups of highly interacting species rather than random associations among palms and frugivores. For nestedness, the $NODF_{Z\text{-}score}$ showed that the Neotropical meta-network is significantly nested before subsampling ($NODF_{Z\text{-}score} > 1.96$) and significantly anti-nested after subsampling ($NODF_{Z\text{-}score} < -1.96$). This could be explained by generalist palm species (e.g., *Euterpe edulis*, *Oneocarpus bataua*, *Syagrus romanzoffiana* and *Mauritia flexuosa*) that have wider geographic distributions than the frugivores they interact with. Random subsampling then creates networks that have more exclusive links between palm and frugivores than in the meta-network. This is also reflected in the large variance observed in the subsampled $NODF_{Z\text{-}score}$ and consistent with the persistent modular structure after subsampling. In the Afrotropical meta-network, the observed anti-nested pattern might arise because recorded palm–frugivore interactions are geographically widespread but regionally clustered, for example, reflecting Madagascar as well as distinct biogeographical subregions in Africa (i.e., the Congolian, Zambezian, and Southern African region) (Linder et al., 2012).

We found a positive relationship between palm fruit size and frugivore body size in the Afrotropics, suggesting morphological trait matching between these mutualistic partners (Bender et al., 2018). This relationship was not statistically significant in the Neotropics. This contrasts with results from a locally sampled, hyperdiverse seed dispersal network in the Neotropics where the relationship between frugivore body size and plant fruit size is driven by differences in body size between birds and mammals (i.e., birds predominantly disperse small fruits whereas mammals predominantly disperse large fruits) (Donatti et al., 2011). The lack of a broad-scale, Neotropical size-matching relationship in our study could be driven, at least partly, by the late Quaternary loss of mammalian megafauna, which was particularly pronounced in the Neotropics (Janzen & Martin, 1982; Pires, Guimarães, Galetti, & Jordano, 2018; Svenning et al., 2016). This could have resulted in an increased extinction rate of palms with megafaunal fruits (Onstein et al., 2018). After these Pleistocene megafauna extinctions, Neotropical scatter-hoarding rodents seem to have substituted to some degree the extinct megafauna seed dispersers of large-seeded trees such as palms (Guimarães, Galetti, & Jordano, 2008; Jansen et al.,

2012; Pires et al., 2018). In the Afrotropics, a positive relationship between palm fruit size and frugivore body size was retained when analysing birds and mammals separately, which corresponds to the few megafauna extinctions in this regions (Svenning et al., 2016). The morphological (size) matching relationship between frugivorous birds and fleshy-fruited plants may be caused by avian body mass being correlated with avian gape size which imposes a strong selective pressure on fruit ingestability (Burns & Lake, 2009; Jordano, 1995; Lord, 2004). Studies of plant–frugivore networks across the Neotropical Andes further show that trait matching between birds and fleshy-fruited plants can also be found for other trait combinations such as plant crop mass and avian body mass (Bender et al., 2018). However, only a few palm species occur at high elevations and data on crop masses of palms are rare, making it difficult to specifically test this trait matching relationship for palms.

Our study exemplifies the Eltonian shortfall, that is, the incomplete and limited knowledge of species interactions we currently have (Hortal et al., 2015). Despite aggregating 750 unique pairwise interaction records for 340 frugivores and 126 palms, extensive knowledge gaps remain in terms of taxonomic and geographic coverage of palm–frugivore interactions (Figure 3). The low coverage and sampling completeness of available data further provide an incentive to increase our baseline knowledge of palm–frugivore seed dispersal interactions, for example, through targeted field work as well as further data mining. For instance, additional interaction data could be retrieved by (a) expanding empirical field data through mobilizing citizen science projects (Poelen et al., 2014); (b) utilizing more advanced text mining tools that can find biological information (e.g., on species interactions) through searches of taxon names in machine-readable texts (Thessen & Parr, 2014); and (c) broaden the literature search by querying not only the WoS, but also other databases (e.g., Google Scholar, Scopus) or unpublished information (e.g., theses that are only available in local university repositories, interaction data from dedicated homepages). A bottleneck of our current data extraction framework (Figure 1) is that the title and abstract screening (via the graphical user interface of the R package 'metagear') as well as the manual full text scans of articles are costly and labour-intensive. Hence, a promising next step could be to develop text mining tools that allow automated content analysis to extract ecologically relevant information from high volumes of literature (Nunez-Mir, Iannone, Pijanowski, Kong, & Fei, 2016). However, in the context of species interactions this requires not only to automatically identify entities in the text (i.e., species names), but also how they are related (e.g., species A disperses species B) (Skusa et al., 2005; Thessen & Parr, 2014). To our knowledge, user-friendly software that allows such text mining of species interaction data is not yet available.

As a contribution towards increasing the digital accessibility of species interaction data, following the FAIR (findability, accessibility, interoperability, and reusability) principles (Wilkinson et al., 2016), we make our palm–frugivore dataset not only available in the DRYAD digital repository (https://doi.org/10.5061/dryad.rd46vq3), but also through the Global Biotic Interactions (GloBI) infrastructure (see Data accessibility). This allows to standardize the extracted interaction data and to integrate them with available taxonomies, ontologies, and vocabularies (Poelen et al., 2014). For instance, the GloBI infrastructure applies the Open Biomedical Ontologies (OBO) Relations Ontology (Smith et al., 2005) which uses defined interaction terms to describe how species interact with each other (e.g., the Brazilian Tapir *Tapirus terrestris* "eats" the palm *Oenocarpus mapora*, the palm *Attalea humilis* is "eatenBy" the collared peccary *Pecari tajacu*). This standardizes not only the terms for recording species interaction data, but also allows to link and cross-reference these interaction records with several taxonomies and name services, with other ontologies that describe environments and habitats, and with standardized information on locations and geographic names (Poelen et al., 2014).

5 | CONCLUSIONS

Our synthesis of palm–frugivore interactions reveals distinct biogeographical differences in animal-mediated seed dispersal of palms. In the Afrotropics, the lower interaction diversity relative to the Neotropics parallels the low taxonomic diversity previously reported for the Afrotropical flora and fauna (Fleming & Kress, 2013; Fleming et al., 1987; Kissling et al., 2009, 2012; Richards, 1973). Network indices such as modularity and nestedness suggest a non-random arrangement of seed dispersal meta-networks in both biogeographical regions, with stronger modularity in the Neotropics than the Afrotropics. We hypothesize that the lack of broad-scale morphological trait matching among Neotropical palms and avian and mammalian frugivores, respectively, could be partly driven by the extinction of megafauna (Guimarães et al., 2008; Janzen & Martin, 1982) and a subsequent replacement of primary seed dispersal through secondary seed dispersal by scatter-hoarding rodents (Jansen et al., 2012). We suggest that deeper insights into the biogeography of species interactions could be obtained through additional data mining and targeted field work. We therefore urge ecologists and biogeographers to collect and aggregate more species interaction data, and to make them findable, accessible, and reusable through open-data repositories and interoperable web services.

ACKNOWLEDGEMENTS

G.M. thanks SENESCYT (Secretaria Nacional de Educación Superior, Ciencia y Tecnología) of Ecuador for financial support via a scholarship for MSc studies (Convocatoria Abierta 2014 I Fase). K.T. was financially supported by the AAU Talent Programme. W.D.K. was supported by a University of Amsterdam starting grant, the University of Amsterdam Faculty Research Cluster "Global Ecology," and grant 824.15.007 from the Netherlands Organisation for Scientific Research (NWO).

DATA ACCESSIBILITY

All palm–frugivore interaction data extracted for this study are available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.rd46vq3) and from the Global Biotic Interactions (GloBI) infrastructure (https://www.globalbioticinteractions.org/). In GloBI, our

dataset can be located by entering the dataset name 'globi:fgabriel1891/Palm-Frugivore_Interactions_Neo-Afrotropics' into the field "according to." This will provide all individual interaction records with their original sources. The dataset can also be directly accessed from GloBI via the following link: https://www.globalbioticinteractions.org/?accordingTo=globi%3Afgabriel1891%2FPalm-Frugivore_Interactions_Neo-Afrotropics&interactionType=interactsWith. Finally, all code to analyse the meta-networks and the trait matching is available from GitHub (https://github.com/fgabriel1891/Palm-frugivore-Interactions-Macroscales).

ORCID

W. Daniel Kissling http://orcid.org/0000-0002-7274-6755

REFERENCES

Almeida-Neto, M., Guimarães, P., Guimarães, P. R., Loyola, R. D., & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: Reconciling concept and measurement. *Oikos*, *117*, 1227–1239. https://doi.org/10.1111/j.0030-1299.2008.16644.x

Araújo, M. B., & Rozenfeld, A. (2014). The geographic scaling of biotic interactions. *Ecography*, *37*, 1–10.

Baker, W. J., & Couvreur, T. L. P. (2013). Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. I. Historical biogeography. *Journal of Biogeography*, *40*, 274–285. https://doi.org/10.1111/j.1365-2699.2012.02795.x

Barber, M. J. (2007). Modularity and community detection in bipartite networks. *Physical Review E*, *76*, 066102. https://doi.org/10.1103/PhysRevE.76.066102

Bascompte, J., Jordano, P., Melian, C. J., & Olesen, J. M. (2003). The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 9383–9387. https://doi.org/10.1073/pnas.1633576100

Beaune, D., Bretagnolle, F., Bollache, L., Hohmann, G., Surbeck, M., & Fruth, B. (2013). Seed dispersal strategies and the threat of defaunation in a Congo forest. *Biodiversity and Conservation*, *22*, 225–238. https://doi.org/10.1007/s10531-012-0416-x

Beckett, S. J. (2016). Improved community detection in weighted bipartite networks. *Royal Society Open Science*, *3*, 140536. https://doi.org/10.1098/rsos.140536

Bender, I. M. A., Kissling, W. D., Blendinger, P. G., Böhning-Gaese, K., Hensen, I., Kühn, I., … Schleuning, M. (2018). Morphological trait matching shapes plant-frugivore networks across the Andes. *Ecography*, *41*(11. https://doi.org/10.1111/ecog.03396

BirdLife International (2015). *The BirdLife checklist of the birds of the world, with conservation status and taxonomic sources*. Version 8. Available at: http://datazone.birdlife.org/species/taxonomy (accessed October 2015).

Brummitt, R. K. (2001). *World Geographical Scheme for Recording Plant Distributions*, 2nd ed.. Pittsburgh: Hunt Institute for Botanical Documentation Carnegie Mellon University.

Burns, K. C., & Lake, B. (2009). Fruit-frugivore interactions in two southern hemisphere forests: allometry, phylogeny and body size. *Oikos*, *118*, 1901–1907. https://doi.org/10.1111/j.1600-0706.2009.17661.x

Chamberlain, S., & Szöcs, E. (2013). taxize: taxonomic search and retrieval in R. *F1000Research*, *2*, 191.

Chao, A., Colwell, R. K., Lin, C.-W., & Gotelli, N. J. (2009). Sufficient sampling for asymptotic minimum species richness estimators. *Ecology*, *90*, 1125–1133. https://doi.org/10.1890/07-2147.1

de Almeida, A., & Mikich, S. B. (2018). Combining plant–frugivore networks for describing the structure of Neotropical communities. *Oikos*, *127*, 184–197. https://doi.org/10.1111/oik.04774

Dehling, D. M., Jordano, P., Schaefer, H. M., Böhning-Gaese, K., & Schleuning, M. (2016). Morphology predicts species' functional roles and their degree of specialization in plant–frugivore interactions. *Proceedings of the Royal Society of London B: Biological Sciences*, *283*, 20152444. https://doi.org/10.1098/rspb.2015.2444

Donatti, C. I., Guimarães, P. R., Galetti, M., Pizo, M. A., Marquitti, F. M. D., & Dirzo, R. (2011). Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. *Ecology Letters*, *14*, 773–781. https://doi.org/10.1111/j.1461-0248.2011.01639.x

Dormann, C. F., Fründ, J., Blüthgen, N., & Gruber, B. (2009). Indices, graphs and null models: analyzing bipartite ecological networks. *The Open Ecology Journal*, *2*, 7–24. https://doi.org/10.2174/1874213000902010007

Dransfield, J., Uhl, N. W., Asmussen, C. B., Baker, W. J., Harley, M. M., & Lewis, C. E. (2008). *Genera palmarum—The evolution and classification of palms*. Richmond, UK: Royal Botanical Gardens, Kew.

Dunning, J. B. (2008). *Handbook of avian body masses* (2nd ed.). Boca Raton: CRC Press.

Eiserhardt, W. L., Svenning, J.-C., Kissling, W. D., & Balslev, H. (2011). Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. *Annals of Botany*, *108*, 1391–1416. https://doi.org/10.1093/aob/mcr146

Eklöf, A., Jacob, U., Kopp, J., Bosch, J., Castro-Urgal, R., Chacoff, N. P., … Allesina, S. (2013). The dimensionality of ecological networks. *Ecology Letters*, *16*, 577–583. https://doi.org/10.1111/ele.12081

Fleming, T. H., Breitwisch, R., & Whitesides, G. H. (1987). Patterns of tropical vertebrate frugivore diversity. *Annual Review of Ecology and Systematics*, *18*, 91–109. https://doi.org/10.1146/annurev.es.18.110187.000515

Fleming, T. H., & Kress, W. J. (2013). *The ornaments of life: coevolution and conservation in the tropics*. Chicago: Chicago University Press. https://doi.org/10.7208/chicago/9780226023328.001.0001

Fortuna, M. A., Stouffer, D. B., Olesen, J. M., Jordano, P., Mouillot, D., Krasnov, B. R., … Bascompte, J. (2010). Nestedness versus modularity in ecological networks: two sides of the same coin? *Journal of Animal Ecology*, *79*, 811–817.

Göldel, B., Kissling, W. D., & Svenning, J.-C. (2015). Geographical variation and environmental correlates of functional trait distributions in palms (Arecaceae) across the New World. *Botanical Journal of the Linnean Society*, *179*, 602–617. https://doi.org/10.1111/boj.12349

Gotelli, N. J., & Colwell, R. K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, *4*, 379–391. https://doi.org/10.1046/j.1461-0248.2001.00230.x

Govaerts, R., & Dransfield, J. (2005). *World checklist of palms*. Richmond, UK: Royal Botanic Gardens Kew.

Guimarães, P. R. Jr., Galetti, M., & Jordano, P. (2008). Seed dispersal anachronisms: rethinking the fruits extinct megafauna ate. *PLoS ONE*, *3*, e1745. https://doi.org/10.1371/journal.pone.0001745

Hagen, M., Kissling, W. D., Rasmussen, C., De Aguiar, M. A. M., Brown, L. E., Carstensen, D. W., … Olesen, J. M. (2012). Biodiversity, species interactions and ecological networks in a fragmented world. *Advances in Ecological Research*, *46*, 89–210. https://doi.org/10.1016/B978-0-12-396992-7.00002-2

Henderson, A. (2002). *Evolution and ecology of palms*. Bronx: The New York Botanical Garden Press.

Horn, M. H., Correa, S. B., Parolin, P., Pollux, B. J. A., Anderson, J. T., Lucas, C., … Goulding, M. (2011). Seed dispersal by fishes in tropical and temperate fresh waters: The growing evidence. *Acta Oecologica*, *37*, 561–577. https://doi.org/10.1016/j.actao.2011.06.004

Hortal, J., Bello, F. D., Diniz-Filho, J. A. F., Lewinsohn, T. M., Lobo, J. M., & Ladle, R. J. (2015). Seven shortfalls that beset large-scale knowledge of

biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *46*, 523–549. https://doi.org/10.1146/annurev-ecolsys-112414-054400

IUCN, Conservation International, Arizona State University, Texas A&M University, University of Rome, University of Virginia & Zoological Society London (2008). *An analysis of mammals on the 2008 IUCN Red List*. Available at: http://www.iucnredlist.org/initiatives/mammals (accessed October 2016).

Jansen, P. A., Hirsch, B. T., Emsens, W.-J., Zamora-Gutierrez, V., Wikelski, M., & Kays, R. (2012). Thieving rodents as substitute dispersers of megafaunal seeds. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 12610–12615. https://doi.org/10.1073/pnas.1205184109

Janzen, D. H., & Martin, P. S. (1982). Neotropical anachronism—The fruits the Gomphotheres ate. *Science*, *215*, 19–27. https://doi.org/10.1126/science.215.4528.19

Jordano, P. (1995). Angiosperm fleshy fruits and seed dispersers—A comparative analysis of adaptation and constraints in plant-animal interactions. *American Naturalist*, *145*, 163–191. https://doi.org/10.1086/285735

Jordano, P. (2000). Fruits and frugivory. In M. Fenner (Ed.), *Seeds: the ecology of regeneration in plant communities* (pp. 125–165). Wallingford, UK: CABI Publishing. https://doi.org/10.1079/9780851994321.0000

Kissling, W. D. (2017). Has frugivory influenced the macroecology and diversification of a tropical keystone plant family? *Research Ideas and Outcomes*, *3*, e14944. https://doi.org/10.3897/rio.3.e14944

Kissling, W. D., Baker, W. J., Balslev, H., Barfod, A. S., Borchsenius, F., Dransfield, J., … Svenning, J.-C. (2012). Quaternary and pre-Quaternary historical legacies in the global distribution of a major tropical plant lineage. *Global Ecology and Biogeography*, *21*, 909–921. https://doi.org/10.1111/j.1466-8238.2011.00728.x

Kissling, W. D., Böhning-Gaese, K., & Jetz, W. (2009). The global distribution of frugivory in birds. *Global Ecology and Biogeography*, *18*, 150–162. https://doi.org/10.1111/j.1466-8238.2008.00431.x

Kissling, W. D., Dalby, L., Fløjgaard, C., Lenoir, J., Sandel, B., Sandom, C., … Svenning, J.-C. (2014). Establishing macroecological trait datasets: Digitalization, extrapolation, and validation of diet preferences in terrestrial mammals worldwide. *Ecology and Evolution*, *4*, 2913–2930. https://doi.org/10.1002/ece3.1136

Kissling, W. D., & Schleuning, M. (2015). Multispecies interactions across trophic levels at macroscales: Retrospective and future directions. *Ecography*, *38*, 346–357. https://doi.org/10.1111/ecog.00819

Lajeunesse, M. J. (2015). Facilitating systematic reviews, data extraction and meta-analysis with the metagear package for R. *Methods in Ecology and Evolution*, *7*, 323–330.

Linder, H. P., de Klerk, H. M., Born, J., Burgess, N. D., Fjeldså, J., & Rahbek, C. (2012). The partitioning of Africa: statistically defined biogeographical regions in sub-Saharan Africa. *Journal of Biogeography*, *39*, 1189–1205. https://doi.org/10.1111/j.1365-2699.2012.02728.x

Lord, J. M. (2004). Frugivore gape size and the evolution of fruit size and shape in southern hemisphere floras. *Austral Ecology*, *29*, 430–436. https://doi.org/10.1111/j.1442-9993.2004.01382.x

Mack, A. L. (1993). The sizes of vertebrate-dispersed fruits—A Netropical-Paleotropical comparison. *American Naturalist*, *142*, 840–856. https://doi.org/10.1086/285575

Meyer, C., Kreft, H., Guralnick, R., & Jetz, W. (2015). Global priorities for an effective information basis of biodiversity distributions. *Nature Communications*, *6*, 8221. https://doi.org/10.1038/ncomms9221

Nunez-Mir, G. C., Iannone, B. V., Pijanowski, B. C., Kong, N., & Fei, S. (2016). Automated content analysis: Addressing the big literature challenge in ecology and evolution. *Methods in Ecology and Evolution*, *7*, 1262–1272. https://doi.org/10.1111/2041-210X.12602

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., O'Hara, R. B., Simpson, G. L., … Wagner, H. (2007). *vegan: Community Ecology Package*. R package. Available at: https://cran.r-project.org/web/packages/vegan/index.html (accessed October 2016).

Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 19891–19896. https://doi.org/10.1073/pnas.0706375104

Onstein, R. E., Baker, W. J., Couvreur, T. L. P., Faurby, S., Svenning, J.-C., & Kissling, W. D. (2017). Frugivory-related traits promote speciation of tropical palms. *Nature Ecology & Evolution*, *1*, 1903–1911. https://doi.org/10.1038/s41559-017-0348-7

Onstein, R. E., Baker, W. J., Couvreur, T. L. P., Faurby, S., Herrera-Alsina, L., Svenning, J.-C. & Kissling, W. D. (2018). To adapt or go extinct? The fate of megafaunal palm fruits under past global change. *Proceedings of the Royal Society B: Biological Sciences*, *285*, 20180882. https://doi.org/10.1098/rspb.2018.0882

Pires, M. M., Guimarães, P. R., Galetti, M., & Jordano, P. (2018). Pleistocene megafaunal extinctions and the functional loss of long-distance seed-dispersal services. *Ecography*, *41*, 153–163. https://doi.org/10.1111/ecog.03163

Poelen, J. H., Simons, J. D., & Mungall, C. J. (2014). Global biotic interactions: An open infrastructure to share and analyze species-interaction datasets. *Ecological Informatics*, *24*, 148–159. https://doi.org/10.1016/j.ecoinf.2014.08.005

Poisot, T., Gravel, D., Leroux, S., Wood, S. A., Fortin, M.-J., Baiser, B., … Stouffer, D. B. (2016). Synthetic datasets and community tools for the rapid testing of ecological hypotheses. *Ecography*, *39*, 402–408. https://doi.org/10.1111/ecog.01941

Richards, P. W. (1973). Africa, the 'Odd Man Out'. In B. J. Meggers, E. S. Ayensu, & W. D. Duckworth (Eds.), *Tropical forest ecosystems in Africa and South America: a comparative review* (pp. 21–26). Washington, DC: Smithsonian Institution Press.

Rivera-Hutinel, A., Bustamante, R. O., Marín, V. H., & Medel, R. (2012). Effects of sampling completeness on the structure of plant–pollinator networks. *Ecology*, *93*, 1593–1603. https://doi.org/10.1890/11-1803.1

Sandom, C., Dalby, L., Fløjgaard, C., Kissling, W. D., Lenoir, J., Sandel, B., … Svenning, J.-C. (2013). Mammal predator and prey species richness are strongly linked at macroscales. *Ecology*, *94*, 1112–1122. https://doi.org/10.1890/12-1342.1

Schleuning, M., Ingmann, L., Strauß, R., Fritz, S. A., Dalsgaard, B., Matthias Dehling, D., … Dormann, C. F. (2014). Ecological, historical and evolutionary determinants of modularity in weighted seed-dispersal networks. *Ecology Letters*, *17*, 454–463. https://doi.org/10.1111/ele.12245

Skusa, A., Rüegg, A., & Köhler, J. (2005). Extraction of biological interaction networks from scientific literature. *Briefings in Bioinformatics*, *6*, 263–276. https://doi.org/10.1093/bib/6.3.263

Smith, B., Ceusters, W., Klagges, B., Köhler, J., Kumar, A., Lomax, J., … Rosse, C. (2005). Relations in biomedical ontologies. *Genome Biology*, *6*, R46. https://doi.org/10.1186/gb-2005-6-5-r46

Svenning, J.-C., Pedersen, P. B. M., Donlan, C. J., Ejrnæs, R., Faurby, S., Galetti, M., … Vera, F. W. M. (2016). Science for a wilder Anthropocene: Synthesis and future directions for trophic rewilding research. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 898–906. https://doi.org/10.1073/pnas.1502556112

Tella, J. L., Baños-Villalba, A., Hernández-Brito, D., Rojas, A., Pacífico, E., Díaz-Luque, J. A., … Hiraldo, F. (2015). Parrots as overlooked seed dispersers. *Frontiers in Ecology and the Environment*, *13*, 338–339. https://doi.org/10.1890/1540-9295-13.6.338

Thessen, A. E., & Parr, C. S. (2014). Knowledge extraction and semantic annotation of text from the Encyclopedia of Life. *PLoS ONE*, *9*, e89550. https://doi.org/10.1371/journal.pone.0089550

Trøjelsgaard, K., & Olesen, J. M. (2013). Macroecology of pollination networks. *Global Ecology and Biogeography*, *22*, 149–162. https://doi.org/10.1111/j.1466-8238.2012.00777.x

Wilkinson, M. D., Dumontier, M., Aalbersberg, I. J., Appleton, G., Axton, M., Baak, A., … Mons, B. (2016). The FAIR Guiding Principles for scientific data management and stewardship. *Scientific Data*, *3*, 160018. https://doi.org/10.1038/sdata.2016.18

Zanata, T. B., Dalsgaard, B., Passos, F. C., Cotton, P. A., Roper, J. J., Maruyama, P. K., … Varassin, I. G. (2017). Global patterns of interaction specialization in bird–flower networks. *Journal of Biogeography*, *44*, 891–910.

Zona, S., & Henderson, A. (1989). A review of animal mediated seed dispersal of palms. *Selbyana*, *11*, 6–21.

BIOSKETCH

Gabriel Muñoz is interested in searching for repeated patterns in the biogeography of nature and the potential use of biodiversity knowledge for the conservation of ecosystems. This article emerged from his MSc research in Ecology and Evolution at the University of Amsterdam (supervised by W. Daniel Kissling) and benefitted from a research stay at Aalborg University (with Kristian Trøjelsgaard). All authors have a particular interest in the biogeography of species interactions.

Author contributions: W.D.K. conceived the idea; W.D.K. and G.M. designed the study; G.M. collected and analysed the data; K.T. and W.D.K. contributed to data analysis; G.M. and W.D.K. wrote the manuscript. All authors contributed to the final manuscript version.

APPENDIX 1

LIST OF DATA SOURCES

Adler, G. H., & Kestell, D. W. (1998). Fates of Neotropical tree seeds influenced by spiny rats (*Proechimys semispinosus*). *Biotropica*, *30*, 677–681.

Aliaga-Rossel, E., & Fragoso, J. M. (2015). Defaunation affects *Astrocaryum gratum* (Arecales: Arecaceae) seed survivorship in a sub-montane tropical forest. *Revista de Biologia Tropical*, *63*, 57–67.

Aliaga-Rossel, E., & Moraes, R. (2014). Mamíferos consumidores de frutas y semillas de la chonta (*Astrocaryum gratum*, Arecaceae) en bosques submontanos y aluviales de Bolivia. *Ecología en Bolivia*, *49*, 98–103.

de Almeida, L. B., & Galetti, M. (2007). Seed dispersal and spatial distribution of *Attalea geraensis* (Arecaceae) in two remnants of Cerrado in Southeastern Brazil. *Acta Oecologica*, *32*, 180–187.

Andrade, P. C., Mota, J. V. L., & Carvalho, A. A. F. (2013). Mutual interactions between frugivorous birds and plants in an urban fragment of Atlantic Forest, Salvador, BA. *Brazilian Journal of Ornithology*, *19*, 12–19.

Andreazzi, C. S., Pimenta, C. S., Pires, A. S., Fernandez, F. A., Oliveira-Santos, L. G., & Menezes, J. F. (2012). Increased productivity and reduced seed predation favor a large–seeded palm in small Atlantic forest fragments. *Biotropica*, *44*, 237–245.

Barbosa, T. A., Barthem, R. B., & Montag, L. F. D. (2015). Feeding ecology of immature *Lithodoras dorsalis* (Valenciennes, 1840) (Siluriformes: Doradidae) in a tidal environment, estuary of the rio Amazonas. *Neotropical Ichthyology*, *13*, 341–348.

Barot, S., Gignoux, J., & Menaut, J. C. (1999). Seed shadows, survival and recruitment: how simple mechanisms lead to dynamics of population recruitment curves. *Oikos*, *86*, 320–330.

de Barros Leite, A., Brancalion, P. H., Guevara, R., & Galetti, M. (2012). Differential seed germination of a keystone palm (*Euterpe edulis*) dispersed by avian frugivores. *Journal of Tropical Ecology*, *28*, 615–618.

Beck, H. (2006). A review of peccary–palm interactions and their ecological ramifications across the Neotropics. *Journal of Mammalogy*, *87*, 519–530.

Beck-King, H., Helversen, O. V., & Beck-King, R. (1999). Home range, population density, and food resources of *Agouti paca* (Rodentia: Agoutidae) in Costa Rica: A study using alternative methods. *Biotropica*, *31*, 675–685.

Beckman, N. G., & Muller-Landau, H. C. (2007). Differential effects of hunting on pre–dispersal seed predation and primary and secondary seed removal of two Neotropical tree species. *Biotropica*, *39*, 328–339.

Birkinshaw, C. (2001). Fruit characteristics of species dispersed by the black lemur (*Eulemur macaco*) in the Lokobe Forest, Madagascar. *Biotropica*, *33*, 478–486.

Bodmer, R. E. (1991). Strategies of seed dispersal and seed predation in Amazonian ungulates. *Biotropica*, *23*, 255–261.

Brancalion, P. H., Rodrigues, R. R., Novembre, A. D., & Gómez, J. M. (2011). Are we misinterpreting seed predation in palms? *Biotropica*, *43*, 12–14.

Brewer, S. W. (2001). Predation and dispersal of large and small seeds of a tropical palm. *Oikos*, *92*, 245–255.

Brewer, S. W., & Rejmánek, M. (1999). Small rodents as significant dispersers of tree seeds in a Neotropical forest. *Journal of Vegetation Science*, *10*, 165–174.

Brewer, S. W., & Webb, M. A. (2001). Ignorant seed predators and factors affecting the seed survival of a tropical palm. *Oikos*, *93*, 32–41.

Browne, L., Ottewell, K., & Karubian, J. (2015). Short–term genetic consequences of habitat loss and fragmentation for the Neotropical palm *Oenocarpus bataua*. *Heredity*, *115*, 389–395.

Bunney, K. (2014). *Seed dispersal in South African trees: With a focus on the megafaunal fruit and their dispersal agents*. Doctoral dissertation, University of Cape Town, South Africa.

Campos, R. C., Steiner, J., & Zillikens, A. (2012). Bird and mammal frugivores of *Euterpe edulis* at Santa Catarina island monitored by camera traps. *Studies on Neotropical Fauna and Environment*, *47*, 105–110.

Cantor, M., Ferreira, L. A., Silva, W. R., & Setz, E. Z. F. (2010). Potential seed dispersal by *Didelphis albiventris* (Marsupialia, Didelphidae) in highly disturbed environment. *Biota Neotropica*, *10*, 45–51.

Carvajal, A., & Adler, G. H. (2008). Seed dispersal and predation by *Proechimys semispinosus* and *Sciurus granatensis* in gaps and understorey in central Panama. *Journal of Tropical Ecology*, *24*, 485–492.

Carvalho, J. S., Vicente, L., & Marques, T. A. (2015). Chimpanzee (Pan troglodytes verus) diet composition and food availability in a human-modified landscape at Lagoas de Cufada Natural Park, Guinea-Bissau. *International Journal of Primatology*, *36*, 802–822.

Castro, E. R. D., & Galetti, M. (2004). Frugivoria e dispersão de sementes pelo lagarto teiú *Tupinambis merianae* (Reptilia: Teiidae). *Papéis Avulsos de Zoologia (São Paulo)*, *44*, 91–97.

Castro, E. R., Galetti, M., & Morellato, L. P. C. (2007). Reproductive phenology of *Euterpe edulis* (Arecaceae) along a gradient in the Atlantic rainforest of Brazil. *Australian Journal of Botany*, *55*, 725–735.

Cestari, C., & Pizo, M. A. (2013). Frugivory by the White–bearded Manakin (*Manacus manacus*, Pipridae) in restinga forest, an ecosystem associated to the Atlantic forest. *Biota Neotropica*, *13*, 345–350.

Chama, L., Berens, D. G., Downs, C. T., & Farwig, N. (2013). Habitat characteristics of forest fragments determine specialisation of plant–frugivore networks in a mosaic forest landscape. *PLoS ONE*, *8*, e54956.

Charles-Dominique, P., Chavez, J., Dubois, M. A., Granville, D., Riera, B., & Vezzoli, C. (2003). Colonization front of the understorey palm *Astrocaryum sciophilum* in a pristine rain forest of French Guiana. *Global Ecology and Biogeography*, *12*, 237–248.

Chaves, O. M., Stoner, K. E., & Arroyo-Rodríguez, V. (2012). Differences in diet between spider monkey groups living in forest fragments and continuous forest in Mexico. *Biotropica*, *44*, 105–113.

Choo, J., Juenger, T. E., & Simpson, B. B. (2012). Consequences of frugivore–mediated seed dispersal for the spatial and genetic structures of a Neotropical palm. *Molecular Ecology*, *21*, 1019–1031.

Christianini, A. V. (2006). Fecundidade, dispersão e predação de sementes de *Archontophoenix cunninghamiana* H. Wendl. & Drude, uma palmeira invasora da Mata Atlântica. *Brazilian Journal of Botany*, *29*, 587–694.

Cid, B., Oliveira-Santos, L. G., & Mourão, G. (2013). Seasonal habitat use of agoutis (*Dasyprocta azarae*) is driven by the palm *Attalea phalerata* in Brazilian Pantanal. *Biotropica*, *45*, 380–385.

Cifuentes, L., Moreno, F., & Arango, D. A. (2013). Comportamiento fenológico de *Euterpe oleracea* (Arecaceae) en bosques inundables del Chocó biogeográfico. *Revista Mexicana de Biodiversidad*, *84*, 591–599.

Cintra, R., & Horna, V. (1997). Seed and seedling survival of the palm *Astrocaryum murumuru* and the legume tree *Dipteryx micrantha* in gaps in Amazonian forest. *Journal of Tropical Ecology*, *13*, 257–277.

Correa, S. B., Araujo, J. K., Penha, J. M., da Cunha, C. N., Stevenson, P. R., & Anderson, J. T. (2015). Overfishing disrupts an ancient mutualism between frugivorous fishes and plants in Neotropical wetlands. *Biological Conservation*, *191*, 159–167.

Correa, S. B., Costa-Pereira, R., Fleming, T., Goulding, M., & Anderson, J. T. (2015). Neotropical fish–fruit interactions: Eco–evolutionary dynamics and conservation. *Biological Reviews*, *90*, 1263–1278.

Correa, S. B., Winemiller, K. O., Lopez-Fernandez, H., & Galetti, M. (2007). Evolutionary perspectives on seed consumption and dispersal by fishes. *AIBS Bulletin*, *57*, 748–756.

Dew, J. L. (2005). Foraging, food choice, and food processing by sympatric ripe–fruit specialists: *Lagothrix lagotricha poeppigii* and *Ateles belzebuth belzebuth*. *International Journal of Primatology*, *26*, 1107–1135.

Dittel, J. W., Lambert, T. D., & Adler, G. H. (2015). Seed dispersal by rodents in a lowland forest in central Panama. *Journal of Tropical Ecology*, *31*, 403–412.

Dudley, J. P. (2000). Seed dispersal by elephants in semiarid woodland habitats of Hwange National Park, Zimbabwe. *Biotropica*, *32*, 556–561.

Eguiarte, L. E., Burquez, A., Rodriguez, J., Martínez-Ramos, M., Sarukhan, J., & Pinero, D. (1993). Direct and indirect estimates of neighborhood and effective population size in a tropical palm, *Astrocaryum mexicanum*. *Evolution*, *47*, 75–87.

Fadini, R. F., Fleury, M., Donatti, C. I., & Galetti, M. (2009). Effects of frugivore impoverishment and seed predators on the recruitment of a keystone palm. *Acta Oecologica*, *35*, 188–196.

Fahr, J., Abedi-Lartey, M., Esch, T., Machwitz, M., Suu-Ire, R., Wikelski, M., & Dechmann, D. K. (2015). Pronounced seasonal changes in the movement ecology of a highly gregarious central–place forager, the African straw–coloured fruit bat (*Eidolon helvum*). *PLoS ONE*, *10*, e0138985.

Felton, A. M., Felton, A., Wood, J. T., & Lindenmayer, D. B. (2008). Diet and feeding ecology of *Ateles chamek* in a Bolivian semihumid forest: The importance of *Ficus* as a staple food resource. *International Journal of Primatology*, *29*, 379–403.

Fleury, M., & Galetti, M. (2006). Forest fragment size and microhabitat effects on palm seed predation. *Biological Conservation*, *131*, 1–13.

Fragoso, J. M. (1997). Tapir-generated seed shadows: Scale-dependent patchiness in the Amazon rain forest. *Journal of Ecology*, *85*, 519–529.

Fragoso, J. M., & Huffman, J. M. (2000). Seed–dispersal and seedling recruitment patterns by the last Neotropical megafaunal element in Amazonia, the tapir. *Journal of Tropical Ecology*, *16*, 369–385.

Fragoso, J., Silvius, K. M., & Correa, J. A. (2003). Long–distance seed dispersal by tapirs increases seed survival and aggregates tropical trees. *Ecology*, *84*, 1998–2006.

Franco-Quimbay, J., & Rojas-Robles, R. (2015). Frugivoría y dispersión de semillas de la palma *Oenocarpus bataua* en dos regiones con diferente estado de conservación. *Actualidades Biológicas*, *37*, 273–285.

Freire, C. C., Closel, M. B., Hasui, E., & Ramos, F. N. (2013). Reproductive phenology, seed dispersal and seed predation in *Syagrus romanzoffiana* in a highly fragmented landscape. *Annales Botanici Fennici*, *50*, 220–228.

de Freitas, C. G., Costa, F. R. C., Svenning, J.-C., & Balslev, H. (2012). Topographic separation of two sympatric palms in the central Amazon – does dispersal play a role? *Acta Oecologica*, *39*, 128–135.

Galetti, M., & Aleixo, A. (1998). Effects of palm heart harvesting on avian frugivores in the Atlantic rain forest of Brazil. *Journal of Applied Ecology*, *35*, 286–293.

Galetti, M., Donatti, C. I., Pizo, M. A., & Giacomini, H. C. (2008). Big fish are the best: seed dispersal of *Bactris glaucescens* by the pacu fish (*Piaractus mesopotamicus*) in the Pantanal, Brazil. *Biotropica*, *40*, 386–389.

Galetti, M., Donatti, C. I., Steffler, C., Genini, J., Bovendorp, R. S., & Fleury, M. (2010). The role of seed mass on the caching decision by agoutis, *Dasyprocta leporina* (Rodentia: Agoutidae). *Zoologia Curitiba*, *27*, 472–476.

Galetti, M., & Guimarães, P. R. Jr (2013). Seed dispersal of *Attalea phalerata* (Palmae) by Crested caracaras (*Caracara plancus*) in the Pantanal and a review of frugivory by raptors. *Brazilian Journal of Ornithology*, *12*, 133–135.

Gálvez, D. (2011). Digestibility of palm seeds and bruchids larvae by Neotropical rodents. *Animal Biology*, *61*, 21–27.

Gálvez, D., & Jansen, P. A. (2007). Bruchid beetle infestation and the value of *Attalea butyracea* endocarps for Neotropical rodents. *Journal of Tropical Ecology*, *23*, 381–384.

Galvez, D., Kranstauber, B., Kays, R. W., & Jansen, P. A. (2009). Scatter hoarding by the Central American agouti: a test of optimal cache spacing theory. *Animal Behaviour*, *78*, 1327–1333.

Garzon-Lopez, C. X., Ballesteros-Mejia, L., Ordoñez, A., Bohlman, S. A., Olff, H., & Jansen, P. A. (2015). Indirect interactions among tropical tree species through shared rodent seed predators: a novel mechanism of tree species coexistence. *Ecology Letters*, *18*, 752–760.

Gatti, A., Bianchi, R., Rosa, C. R. X., & Mendes, S. L. (2006). Diet of two sympatric carnivores, *Cerdocyon thous* and *Procyon cancrivorus*, in a restinga area of Espirito Santo State, Brazil. *Journal of Tropical Ecology*, *22*, 227–230.

Genini, J., Galetti, M., & Morellato, L. P. (2009). Fruiting phenology of palms and trees in an Atlantic rainforest land-bridge island. *Flora*, *204*, 131–145.

Giombini, M. I., Bravo, S. P., & Martinez, M. F. (2009). Seed dispersal of the palm *Syagrus romanzoffiana* by tapirs in the semi-deciduous Atlantic Forest of Argentina. *Biotropica*, *41*, 408–413.

González-Zamora, A., Arroyo-Rodríguez, V., Chaves, Ó. M., Sánchez-López, S., Stoner, K. E., & Riba-Hernández, P. (2009). Diet of spider monkeys (*Ateles geoffroyi*) in Mesoamerica: current knowledge and future directions. *American Journal of Primatology*, *71*, 8–20.

Grenha, V., Macedo, M. V., Pires, A. S., & Monteiro, R. F. (2010). El papel de *Cerradomys subflavus* (Rodentia, Cricetidae) como depredador y dispersor de semillas de la palma *Allagoptera arenaria*. *Mastozoología Neotropical*, *17*, 61–68.

Guix, J. C., & Ruiz, X. (1995). Toucans and thrushes as potential dispersers of seed-predatory weevil larvae in southeastern Brazil. *Canadian Journal of Zoology*, *73*, 745–748.

Guix, J. C., & Ruiz, X. (1997). Weevil larvae dispersal by guans in south-eastern Brazil. *Biotropica*, *29*, 522–525.

Guzmán, A., & Stevenson, P. R. (2008). Seed dispersal, habitat selection and movement patterns in the Amazonian tortoise, *Geochelone denticulata*. *Amphibia-Reptilia*, *29*, 463–472.

Hernandez, A. (2011). Internal dispersal of seed–inhabiting insects by vertebrate frugivores: a review and prospects. *Integrative Zoology*, *6*, 213–221.

Hirsch, B. T., Kays, R., & Jansen, P. A. (2012). A telemetric thread tag for tracking seed dispersal by scatter–hoarding rodents. *Plant Ecology*, *213*, 933–943.

Hirsch, B. T., Kays, R., Pereira, V. E., & Jansen, P. A. (2012). Directed seed dispersal towards areas with low conspecific tree density by a scatter–hoarding rodent. *Ecology Letters*, *15*, 1423–1429.

Hoch, G. A., & Adler, G. H. (1997). Removal of black palm (*Astrocaryum standleyanum*) seeds by spiny rats (*Proechimys semispinosus*). *Journal of Tropical Ecology*, *13*, 51–58.

Horn, M. H., Correa, S. B., Parolin, P., Pollux, B. J. A., Anderson, J. T., Lucas, C., Widmann, P., Tjiu, A., Galetti, M., & Goulding, M. (2011). Seed dispersal by fishes in tropical and temperate fresh waters: the growing evidence. *Acta Oecologica*, *37*, 561–577.

Jansen, P. A., Elschot, K., Verkerk, P. J., & Wright, S. J. (2010). Seed predation and defleshing in the agouti–dispersed palm *Astrocaryum standleyanum*. *Journal of Tropical Ecology*, *26*, 473–480.

Jansen, P. A., Hirsch, B. T., Emsens, W. J., Zamora-Gutierrez, V., Wikelski, M., & Kays, R. (2012). Thieving rodents as substitute dispersers of megafaunal seeds. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 12610–12615.

Jansen, P. A., Visser, M. D., Joseph, W. S., Rutten, G., & Muller-Landau, H. C. (2014). Negative density dependence of seed dispersal and seedling recruitment in a Neotropical palm. *Ecology Letters*, *17*, 1111–1120.

Jorge, M. L. S., & Howe, H. F. (2009). Can forest fragmentation disrupt a conditional mutualism? A case from central Amazon. *Oecologia*, *161*, 709–718.

Kahn, F., & de Granville, J.-J. (1992). *Palm communities in the forest ecosystems of Amazonia*. Berlin Heidelberg, Berlin, Heidelberg: Springer.

Karubian, J., Duraes, R., Storey, J. L., & Smith, T. B. (2012). Mating behavior drives seed dispersal by the long–wattled umbrellabird *Cephalopterus penduliger*. *Biotropica*, *44*, 689–698.

Karubian, J., Ottewell, K., Link, A., & Di Fiore, A. (2015). Genetic consequences of seed dispersal to sleeping trees by white–bellied spider monkeys. *Acta Oecologica*, *68*, 50–58.

Karubian, J., Sork, V. L., Roorda, T., Duraes, R., & Smith, T. B. (2010). Destination–based seed dispersal homogenizes genetic structure of a tropical palm. *Molecular Ecology*, *19*, 1745–1753.

Keuroghlian, A., & Eaton, D. P. (2008). Fruit availability and peccary frugivory in an isolated Atlantic forest fragment: effects on peccary ranging behavior and habitat use. *Biotropica*, *40*, 62–70.

Keuroghlian, A., & Eaton, D. P. (2009). Removal of palm fruits and ecosystem engineering in palm stands by white–lipped peccaries (*Tayassu pecari*) and other frugivores in an isolated Atlantic Forest fragment. *Biodiversity and Conservation*, *18*, 1733.

Klinger, R., & Rejmánek, M. (2009). The numerical and functional responses of a granivorous rodent and the fate of Neotropical tree seeds. *Ecology*, *90*, 1549–1563.

Klinger, R., & Rejmánek, M. (2010). A strong conditional mutualism limits and enhances seed dispersal and germination of a tropical palm. *Oecologia*, *162*, 951–963.

Klinger, R., & Rejmánek, M. (2013). Experimental seed predator removal reveals shifting importance of predation and dispersal limitation in early life history stages of tropical forest trees. *Folia Geobotanica*, *48*, 415–435.

Kristiansen, T., Svenning, J.-C., Eiserhardt, W. L., Pedersen, D., Brix, H., Kristiansen, S., Knadel, M., Grández, C., & Balslev, H. (2012). Environment versus dispersal in the assembly of western Amazonian palm communities. *Journal of Biogeography*, *39*, 1318–1332.

Kubitzki, K., & Ziburski, A. (1994). Seed dispersal in flood plain forests of Amazonia. *Biotropica*, *26*, 30–43.

Kuprewicz, E. K. (2013). Mammal abundances and seed traits control the seed dispersal and predation roles of terrestrial mammals in a Costa Rican forest. *Biotropica*, *45*, 333–342.

Kuprewicz, E. K. (2015). Scatter hoarding of seeds confers survival advantages and disadvantages to large–seeded tropical plants at different life stages. *PLoS ONE*, *10*, e0124932.

Lamperti, A. M., French, A. R., Dierenfeld, E. S., Fogiel, M. K., Whitney, K. D., Stauffer, D. J., Holbrook, K. M., Hardesty, B. D., Clark, C. J., Poulsen, J. R., & Wang, B. C. (2014). Diet selection is related to breeding status in two frugivorous hornbill species of Central Africa. *Journal of Tropical Ecology*, *30*, 273–290.

Lazure, L., Bachand, M., Ansseau, C., & Almeida-Cortez, J. S. (2010). Fate of native and introduced seeds consumed by captive white–lipped and collared peccaries (*Tayassu pecari*, Link 1795 and *Pecari tajacu*, Linnaeus 1758) in the Atlantic rainforest, Brazil. *Brazilian Journal of Biology*, *70*, 47–53.

Martins, M. M. (2008). Fruit diet of *Alouatta guariba* and *Brachyteles arachnoides* in Southeastern Brazil: comparison of fruit type, color, and seed size. *Primates*, *49*, 1–8.

Matos, D. M., & Watkinson, A. R. (1998). The fecundity, seed, and seedling ecology of the edible palm *Euterpe edulis* in southeastern Brazil. *Biotropica*, *30*, 595–603.

Mello, M. A., Rodrigues, F. A., Costa, L. D., Kissling, W. D., Şekercioğlu, Ç. H., Marquitti, F. M., & Kalko, E. K. (2015). Keystone species in seed dispersal networks are mainly determined by dietary specialization. *Oikos*, *124*, 1031–1039.

Melo, F. P., Rodriguez-Herrera, B., Chazdon, R. L., Medellin, R. A., & Ceballos, G. G. (2009). Small tent–roosting bats promote dispersal of large–seeded plants in a Neotropical forest. *Biotropica*, *41*, 737–743.

Mendieta-Aguilar, G., Pacheco, L. F., & Roldán, A. I. (2015). Seed dispersal of *Mauritia flexuosa* (Arecaceae) by terretrial frugivores in Laguna Azul, Beni, Bolivia. *Acta Amazonica*, *45*, 45–56.

Mengardo, A. L. T., & Pivello, V. R. (2014). The effects of an exotic palm on a native palm during the first demographic stages: contributions to ecological management. *Acta Botanica Brasilica*, *28*, 552–558.

Mickleburgh, S. P., Hutson, A. M., & Racey, P. A. (1992). *Old World fruit bats. An action plan for their conservation*. Gland, Switzerland: IUCN, pp. 263.

Montúfar, R., Anthelme, F., Pintaud, J. C., & Balslev, H. (2011). Disturbance and resilience in tropical American palm populations and communities. *The Botanical Review*, *77*, 426–461.

Moraes, M. (1991). Contribución al estudio del ciclo biológico de la palma *Copernicia alba* en un área ganadera (Espíritu, Beni, Bolivia). *Ecología en Bolivia*, *18*, 1–20.

Moses, K. L., & Semple, S. (2011). Primary seed dispersal by the black-and-white ruffed lemur (*Varecia variegata*) in the Manombo forest, south-east Madagascar. *Journal of Tropical Ecology*, *27*, 529–538.

Myers, R. L. (2013a). Phenology and growth of *Raphia taedigera* (Arecaceae) in northeastern Costa Rica wetlands. *Revista de Biologia Tropical*, *61*, 35–45.

Myers, R. L. (2013b). Predation, removal and seed dispersal in a wetland dominated by palms (Arecaceae). *Revista de Biologia Tropical*, *61*, 67–85.

O'Farrril, G., Galetti, M., & Campos-Arceiz, A. (2013). Frugivory and seed dispersal by tapirs: an insight on their ecological role. *Integrative Zoology*, *8*, 4–17.

deOliveira, L. C. (1990). *Biologia da reprodução de Allagoptera arenaria* (Gomes) O. Kuntze (*Diplothemium marituum* mart.) Palmae. Doctoral dissertation, Universidade Federal do Rio de Janeiro, Brazil.

Olmos, F., Pardini, R., Boulhosa, R. L., Bürgl, R., & Morsello, C. (1999). Do tapirs steal food from palm seed predators or give them a lift? *Biotropica*, *31*, 375–379.

Palmer, R. R., & Koprowski, J. L. (2014). Feeding behavior and activity patterns of Amazon red squirrels. *Mammalia*, *78*, 303–313.

Piedade, M. T., Parolin, P., & Junk, W. J. (2003). Estratégias de dispersão, produção de frutos e extrativismo da palmeira *Astrocaryum jauari* Mart. nos igapós do Rio Negro: implicações para a ictiofauna. *Ecología Aplicada*, *2*, 32–40.

Pinto, S. R. R., Santos, A. M. M., & Tabarelli, M. (2009). Seed predation by rodents and safe sites for large-seeded trees in a fragment of the Brazilian Atlantic forest. *Brazilian Journal of Biology*, *69*, 763–771.

Pires, A. S., & Galetti, M. (2012). The agouti *Dasyprocta leporina* (Rodentia: Dasyproctidae) as seed disperser of the palm *Astrocaryum aculeatissimum*. *Mastozoología Neotropical*, *19*, 147–153.

Pizo, M. A., & Almeida-Neto, M. (2009). Determinants of fruit removal in *Geonoma pauciflora*, an understory palm of Neotropical forests. *Ecological Research*, *24*, 1179–1186.

Pizo, M. A., & Simão, I. (2001). Seed deposition patterns and the survival of seeds and seedlings of the palm *Euterpe edulis*. *Acta Oecologica*, *22*, 229–233.

Ponce Calderon, M. E. (2002). Patrones de caída de frutos en *Mauritia flexuosa* Lf y fauna involucrada en los procesos de remoción de semillas. *Acta Botánica Venezuelica*, *25*, 119–142.

Poulsen, J. R., Clark, C. J., Connor, E. F., & Smith, T. B. (2002). Differential resource use by primates and hornbills: implications for seed dispersal. *Ecology*, *83*, 228–240.

Puechagut, P. B., Politi, N., Bellis, L. M., & Rivera, L. O. (2013). A disappearing oasis in the semi–arid chaco: Deficient palm regeneration and establishment. *Journal for Nature Conservation*, *21*, 31–36.

Purificação, K. N., Pascotto, M. C., Pedroni, F., Pereira, J. M. N., & Lima, N. A. (2014). Interactions between frugivorous birds and plants in savanna and forest formations of the Cerrado. *Biota Neotropica*, *14*, e20140068.

Quintela, F. M., Iob, G., & Artioli, L. G. (2014). Diet of *Procyon cancrivorus* (Carnivora, Procyonidae) in restinga and estuarine environments of southern Brazil. *Iheringia. Série Zoologia*, *104*, 143–149.

Quiroga-Castro, V. D., & Roldán, A. I. (2001). The fate of *Attalea phalerata* (Palmae) seeds dispersed to a tapir latrine. *Biotropica*, *33*, 472–477.

Ragusa-Netto, J. (2006). Dry fruits and the abundance of the Blue-and-Yellow Macaw (*Ara ararauna*) at a cerrado remnant in central Brazil. *Ornitologia Neotropical*, *17*, 491–500.

Ragusa-Netto, J., & Fecchio, A. (2006). Plant food resources and the diet of a parrot community in a gallery forest of the southern Pantanal (Brazil). *Brazilian Journal of Biology*, *66*, 1021–1032.

Ramírez, B. H., Parrado-Rosselli, Á., & Stevenson, P. (2009). Seed dispersal of a useful palm (*Astrocaryum chambira* Burret) in three Amazonian forests with different human intervention. *Colombia Forestal*, *12*, 5–16.

Ribeiro, L. F., Conde, L. O. M., & Tabarelli, M. (2010). Predation and removal of seeds from five species of palms by *Guerlinguetus ingrami* (Thomas, 1901) in an urban fragment of the Montane Atlantic Forest. *Revista Árvore*, *34*, 637–649.

Rivas, J., Morales, J., & Flores, M. (2001). *El papel de los cracidos (Aves: Galliformes) como dispersores y depredadores de semillas*. Facultad de Ciencias Químicas y Farmacia, Guatemala: Universidad San Carlos de Guatemala.

Rocha, V. J., dos Reis, N. R., & Sekiama, M. L. (2004). Dieta e dispersão de sementes por *Cerdocyon thous* (Linnaeus) (Carnívora, Canidae), em um fragmento florestal no Paraná, Brasil. *Revista Brasileira de Zoologia*, *21*, 871–876.

Rodríguez, M., Delibes, M., & Fedriani, J. M. (2014). Hierarchical levels of seed predation variation by introduced beetles on an endemic Mediterranean palm. *PLoS ONE*, *9*, e109867.

Rojas-Robles, R., Gary Stiles, F., & Muñoz-Saba, Y. (2012). Frugivory and seed dispersal *Oenocarpus bataua* palm (Arecaceae) in a forest from the Colombian Andes. *Revista de Biologia Tropical*, *60*, 1445–1461.

Russo, S. E., Campbell, C. J., Dew, J. L., Stevenson, P. R., & Suarez, S. A. (2005). A multi–forest comparison of dietary preferences and seed dispersal by *Ateles* spp. *International Journal of Primatology*, *26*, 1017–1037.

Sanchez-Cordero, V., & Martinez-Gallardo, R. (1998). Postdispersal fruit and seed removal by forest-dwelling rodents in a lowland rainforest in Mexico. *Journal of Tropical Ecology*, *14*, 139–151.

Santos, A. A., & Ragusa-Netto, J. (2014). Plant food resources exploited by Blue-and-Yellow Macaws (*Ara ararauna*, Linnaeus 1758) at an urban area in Central Brazil. *Brazilian Journal of Biology*, *74*, 429–437.

Sávio Pimentel, D., & Tabarelli, M. (2004). Seed dispersal of the palm *Attalea oleifera* in a remnant of the Brazilian Atlantic Forest. *Biotropica*, *36*, 74–84.

Sazima, I. (2008). The parakeet *Brotogeris tirica* feeds on and disperses the fruits of the palm *Syagrus romanzoffiana* in Southeastern Brazil. *Biota Neotropica*, *8*, 231–234.

Scherbaum, C., & Estrada, A. (2013). Selectivity in feeding preferences and ranging patterns in spider monkeys *Ateles geoffroyi yucatanensis* of northeastern Yucatan peninsula, Mexico. *Current Zoology*, *59*, 125–134.

Scofield, D. G., Smouse, P. E., Karubian, J., & Sork, V. L. (2012). Use of alpha, beta, and gamma diversity measures to characterize seed dispersal by animals. *The American Naturalist*, *180*, 719–732.

Sezen, U. U., Chazdon, R. L., & Holsinger, K. E. (2007). Multigenerational genetic analysis of tropical secondary regeneration in a canopy palm. *Ecology*, *88*, 3065–3075.

Sezen, U. U., Chazdon, R. L., & Holsinger, K. E. (2009). Proximity is not a proxy for parentage in an animal-dispersed Neotropical canopy palm. *Proceedings of the Royal Society of London B: Biological Sciences*, *276*, 2037–2044.

Shapcott, A., Quinn, J., Rakotoarinivo, M., & Dransfield, J. (2012). Contrasting patterns of genetic diversity between two endangered palms with overlapping distributions, *Voanioala gerardii* (Arecoideae) and *Lemurophoenix halleuxii* (Arecoideae), from North-east Madagascar. *Conservation Genetics*, *13*, 1393–1408.

Shapcott, A., Rakotoarinivo, M., Smith, R. J., Lysakova, G., Fay, M. F., & Dransfield, J. (2007). Can we bring Madagascar's critically endangered palms back from the brink? Genetics, ecology and conservation of the critically endangered palm *Beccariophoenix madagascariensis*. *Botanical Journal of the Linnean Society*, *154*, 589–608.

Sica, Y. V., Bravo, S. P., & Giombini, M. I. (2014). Spatial pattern of Pindó palm (*Syagrus romanzoffiana*) recruitment in Argentinian Atlantic forest: The importance of tapir and effects of defaunation. *Biotropica*, *46*, 696–703.

da Silva, F. R., Begnini, R. M., Lopes, B. C., & Castellani, T. T. (2011). Seed dispersal and predation in the palm *Syagrus romanzoffiana* on two islands with different faunal richness, southern Brazil. *Studies on Neotropical Fauna and Environment*, *46*, 163–171.

Silva, G. B. M. D., & Pedroni, F. (2014). Frugivory by birds in cerrado in the city of Uberlândia, Minas Gerais. *Revista Árvore*, *38*, 433–442.

Silva, J. A. M. D., Pereira Filho, M., & Pereira, M. I. D. O. (2003). Valor nutricional e energético de espécies vegetais importantes na alimentação do tambaqui. *Acta Amazonica*, *33*, 687–700.

Silva, M. G., & Tabarelli, M. (2001). Seed dispersal, plant recruitment and spatial distribution of *Bactris acanthocarpa* Martius (Arecaceae) in a remnant of Atlantic forest in northeast Brazil. *Acta Oecologica*, *22*, 259–268.

Silvius, K. M., & Fragoso, J. (2002). Pulp handling by vertebrate seed dispersers increases palm seed predation by bruchid beetles in the northern Amazon. *Journal of Ecology*, *90*, 1024–1032.

Silvius, K. M., & Fragoso, J. M. (2003). Red–rumped agouti (*Dasyprocta leporina*) home range use in an Amazonian forest: implications for the aggregated distribution of forest trees. *Biotropica*, *35*, 74–83.

Smythe, N. (1989). Seed survival in the palm *Astrocaryum standleyanum*: Evidence for dependence upon its seed dispersers. *Biotropica*, *21*, 50–56.

Snow, D. W., & Snow, B. K. (1978). Palm fruits in the diet of the oilbird, *Steatornis caripensis*. *Principes*, *22*, 107–109.

Sório, V. F., Damasceno-Junior, G. A., & Parolin, P. (2014). Dispersal of palm seeds (*Bactris glaucescens* DRUDE) by the fish *Piaractus mesopotamicus* in the Brazilian Pantanal. *Ecotropica*, *20*, 75–82.

Stevenson, P. R., Link, A., González-Caro, S., & Torres-Jiménez, M. F. (2015). Frugivory in canopy plants in a western Amazonian forest: dispersal systems, phylogenetic ensembles and keystone plants. *PLoS ONE*, *10*, e0140751.

Tannenbaum, B., & Wrege, P. (1978). Ecología del guácharo en Venezuela (Steatornis caripensis). *Boletín de la Academia de Ciencias Físicas Matemáticas y Naturales*, *115*, 73–81.

Teresa, M., Piedade, F., Parolin, P., & Junk, W. J. (2006). Phenology, fruit production and seed dispersal of *Astrocaryum jauari* (Arecaceae) in Amazonian black water floodplains. *Revista de Biología Tropical*, *54*, 1171–1178.

Timm, R. M., Lieberman, D., Lieberman, M., & McClearn, D. (2009). Mammals of Cabo Blanco: History, diversity, and conservation after 45 years of regrowth of a Costa Rican dry forest. *Forest Ecology and Management*, *258*, 997–1013.

Tobler, M. W., Janovec, J. P., & Cornejo, F. (2010). Frugivory and seed dispersal by the lowland tapir *Tapirus terrestris* in the Peruvian Amazon. *Biotropica*, *42*, 215–222.

Villalobos, M. P., & Bagno, M. A. (2013). Avian frugivores feeding on *Mauritia flexuosa* (Arecaceae) fruits in Central Brazil. *Brazilian Journal of Ornithology*, *20*, 26–29.

Visser, M. D., Muller-Landau, H. C., Wright, S. J., Rutten, G., & Jansen, P. A. (2011). Tri-trophic interactions affect density dependence of seed fate in a tropical forest palm. *Ecology Letters*, *14*, 1093–1100.

Whitney, K. D., Fogiel, M. K., Lamperti, A. M., Holbrook, K. M., Stauffer, D. J., Hardesty, B. D., Parker, V. T., & Smith, T. B. (1998). Seed dispersal by *Ceratogymna* hornbills in the Dja Reserve, Cameroon. *Journal of Tropical Ecology*, *14*, 351–371.

Whitney, K. D., & Smith, T. B. (1998). Habitat use and resource tracking by African *Ceratogymna* hornbills: implications for seed dispersal and forest conservation. *Animal Conservation*, *1*, 107–117.

Wright, S. J., & Duber, H. C. (2001). Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the palm *Attalea butyraceae*, with implications for tropical tree diversity. *Biotropica*, *33*, 583–595.

Zucaratto, R., & Pires, A. D. S. (2015). Local extinction of an important seed disperser does not modify the spatial distribution of the endemic palm *Astrocaryum aculeatissimum* (Schott) Burret (Arecaceae). *Acta Botanica Brasilica*, *29*, 244–250.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Muñoz G, Trøjelsgaard K, Kissling WD. A synthesis of animal-mediated seed dispersal of palms reveals distinct biogeographical differences in species interactions. *J Biogeogr*. 2019;46:466–484. https://doi.org/10.1111/jbi.13493